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Linkages between stratospheric ozone, UV radiation and climate change and their implications for terrestrial ecosystems

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Abstract

Exposure of plants and animals to ultraviolet-B radiation (UV-B; 280-315 nm) is modified by stratospheric ozone dynamics and climate change. Even though stabilisation and projected recovery of stratospheric ozone is expected to curtail future increases in UV-B radiation at the Earth's surface, on-going changes in climate are increasingly exposing plants and animals to novel combinations of UV-B radiation and other climate change factors (e.g., ultraviolet-A and visible radiation, water availability, temperature and elevated carbon dioxide). Climate change is also shifting vegetation cover, geographic ranges of species, and seasonal timing of development, which further modifies exposure to UV-B radiation. Since our last assessment, there is increased understanding of the underlying mechanisms by which plants perceive UV-B radiation, eliciting changes in growth, development and tolerances of abiotic and biotic factors. However, major questions remain on how UV-B radiation is interacting with other climate change factors to modify the production and quality of crops, as well as important ecosystem processes such as plant and animal competition, pest-pathogen interactions, and the decomposition of dead plant matter (litter). In addition, stratospheric ozone depletion is directly contributing to climate change in the southern hemisphere, such that terrestrial ecosystems in this region are being exposed to altered patterns of precipitation, temperature and fire regimes as well as UV-B radiation. These ozone-driven changes in climate have been implicated in both increases and reductions in the growth, survival and reproduction of plants and animals in Antarctica, South America and New Zealand. In this assessment, we summarise advances in our knowledge of these and other linkages and effects, and identify uncertainties and knowledge gaps that limit our ability to fully evaluate the ecological consequences of these environmental changes on terrestrial ecosystems.

3.1 Introduction and overview

The structure, function and diversity of terrestrial ecosystems are being modifed by ongoing changes in the Earth's climate, and these complex changes are becoming increasingly evident with time.[1-3] An assessment of the effects of depletion and recovery of stratospheric ozone and associated changes in ultraviolet-B radiation (UV-B, 280-315 nm) on the terrestrial biota must, therefore, consider the role of climate change in the response of these organisms and ecosystems. In some regions, stratospheric ozone depletion is itself contributing to climate change with the result that ecosystems are being affected by the consequent ozone-driven changes in temperature and precipitation.[4, 5] Prior assessments have considered the effects of stratospheric ozone depletion in the context of climate change and have reported on some of the ways in which climate change can potentially interact with ozone depletion and UV-B radiation to modify terrestrial ecosystem function and composition.[6-8] In this assessment, we report on progress made since the last one[8] and examine and further explore recent findings that document interactive effects of ozone depletion, UV-B radiation and climate change on terrestrial organisms and ecosystems, including cultivated species and highly managed ecosystems (e.g., agroecosystems). We emphasise effects that have, at least to some degree, been demonstrated to occur in nature, but also identify areas where potential effects on terrestrial ecosystems could occur in the future. Where possible, areas of uncertainty are addressed, and the significance of findings is placed in a context relevant to policy makers.

Ecologically significant linkages between stratospheric ozone depletion, climate change and UV radiation are diverse, sometimes bi-directional, and, in certain cases, exhibit important feedbacks to the climate system (Fig. 1). However, climate change is increasingly contributing to changes in the timing and duration of UV-B radiation exposure, independent of ozone dynamics. These changes can occur in a number of ways (see section 3.7). One avenue involves climate change-driven shifts in cloud cover, which is increasing in some regions (usually wetter areas), while decreasing in others (usually drier regions).[1, 4] Similarly, climate change-driven effects on vegetation (e.g., forest die-back or shrub invasions) can increase or decrease the UV exposure conditions of understory plants and animals. As a result of warmer growth conditions and altered timing of seasons, many plants are initiating growth and flowering earlier in the year,[9, 10] while certain animals are adjusting their timing of breeding and migration.[11, 12] As UV-B radiation varies seasonally (Fig. 8), a change in the timing of important life-cycle events can easily affect their exposure to UV-B radiation. In addition, the geographic ranges of many plants and animals, including wild and domesticated species, are shifting to higher elevations and latitudes in response to climate change.[1, 2, 13-15] Because of existing natural altitudinal and latitudinal gradients in solar UV radiation,[4, 16-18] these changes in geographic ranges can potentially increase (at high elevations) or decrease (at high

latitudes) the amount of UV-B radiation received by organisms. Unlike ozone depletion, all of the above climate change-driven effects are modifying organisms' exposure to the full solar radiation spectrum at the Earth's surface, including UV-B as well as UV-A (315-400 nm) and visible (400-700 nm) radiation. At the same time, plants and animals are being exposed to novel combinations of UV radiation with other abiotic (e.g., changing day length, and fluctuating temperatures) and biotic factors (e.g., competitors, pests, and pollinators). Because of these complexities, it is necessary to consider how organism and ecosystem responses to UV-B radiation are modified by concomitant changes in other regions of the solar spectrum (i.e., UV-A and visible radiation) as well as simultaneous changes in a diverse range of abiotic and biotic factors.

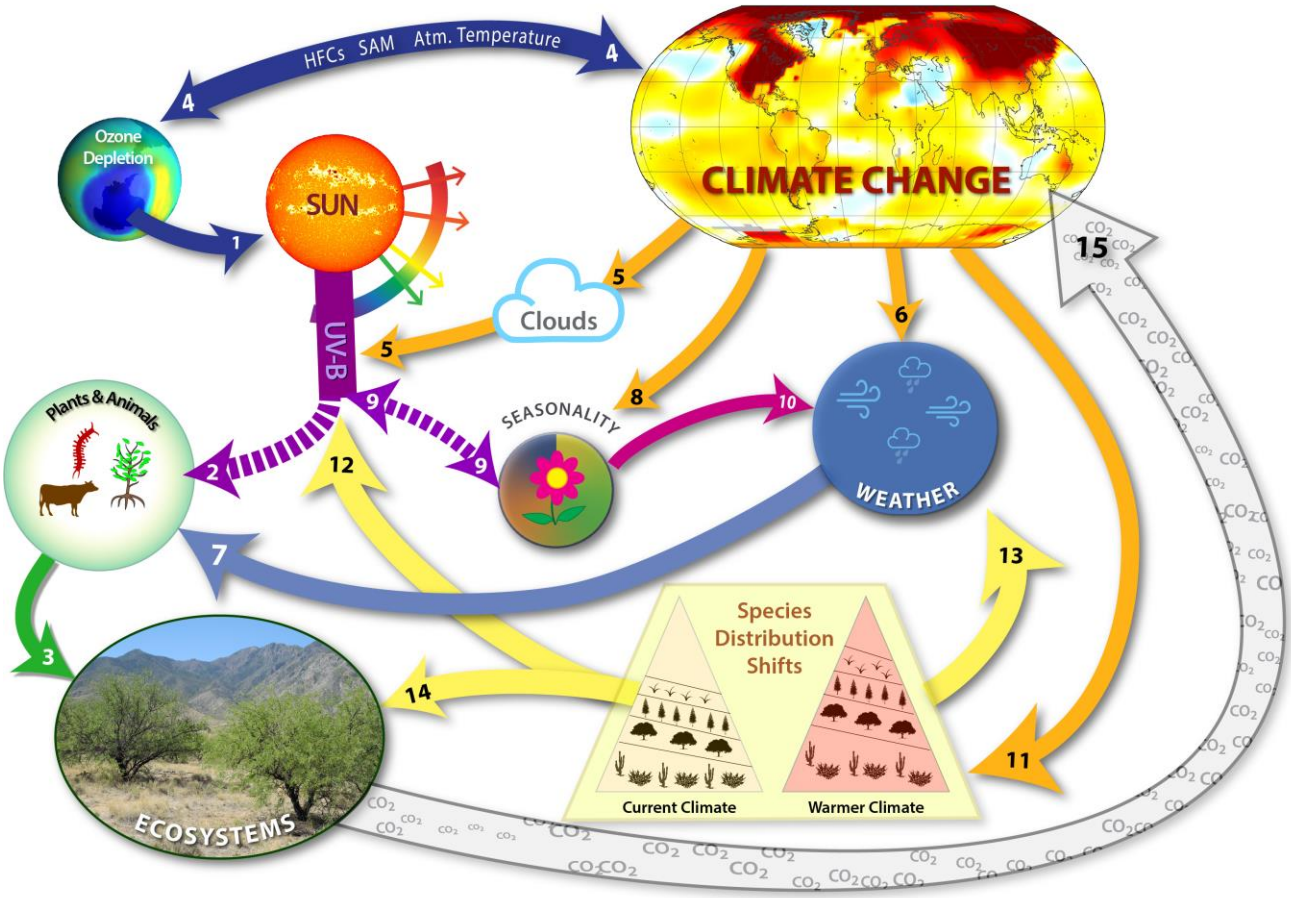
Solar UV radiation (UV-B and UV-A) is known to affect the growth and performance of terrestrial plants and animals (see sections 3.3 and 3.4). The shorter wavelengths of UV radiation (mostly in the UV-B range) may cause cellular damage, and this can lead to changes in an organism's morphology, physiology, and biochemistry. Concurrent exposure to longer wavelengths (e.g., UV-A and/or visible radiation), however, can often reduce the negative effects of UV-B radiation.[19] In addition, both UV-B and UV-A radiation are important sources of information for plants and animals. This radiation is perceived by specific photoreceptors, which trigger a range of responses. Many animals sense UV radiation and avoid exposure to prolonged periods of high UV-B radiation.[20, 21] These behavioural responses together with physiological mechanisms can mitigate some of the negative outcomes of high UV-B radiation. In some animal species (e.g., insects and birds), UV radiation is used as a visual cue that enhances foraging, mate selection or other behavioural activities.[21] By comparison, land plants are sessile (rooted to their growth medium) and require sunlight for photosynthesis and growth. Their primary response to changing UV radiation conditions typically involves acclimating or adapting to these changes using biochemical and physiological mechanisms. However, like animals, plants can sense UV radiation in their surroundings, which has adaptive value.[22]

Many initial studies following the discovery of the Antarctic ozone hole (as reviewed by Aphalo*, et al.* [23], Björn [24], Barnes [25]) emphasised the direct, detrimental effects of increased UV-B radiation on plants, especially important food crops. However, most evidence to date indicates that, under realistic exposures, the direct, damaging effects of high UV-B radiation on photosynthesis, plant productivity and crop yield, are relatively minor.[7, 26-30] More recent studies have focused on understanding how plants a) respond to UV radiation against the backdrop of a rapidly changing climate in conjunction with current and projected stratospheric ozone dynamics; and b) perceive the UV-B radiation and what role this radiation plays in regulating growth and development.[31-34] At present, it is widely accepted that UV-B radiation can have beneficial as well as unfavourable effects on plants.[27, 35-37] In some cases, reduced exposure to UV-B radiation can even have negative

consequences for plant performance, pest defence,[38] and food quality.[39] Thus, projected recovery of stratospheric ozone to levels that may exceed those in the recent past (i.e., 1970's;[4, 40]), means that there is a need to fully evaluate how organisms and ecosystems will respond to the increases and decreases in solar UV-B radiation that occur in conjunction with a rapidly changing climate.

Climate change alters regional weather patterns, including temperature and precipitation, and these changes can directly affect plants and ecosystems by altering moisture availability and critical thermal conditions for growth, reproduction and survival. Of interest in this assessment, however, is how climate change-driven plant responses are modified by UV radiation (see section 3.3). Exposure to UV-B radiation can enhance plant tolerance to some abiotic factors (e.g., water and temperature stress) [41], while other factors may alter the sensitivity of plants to UV radiation. However, these effects are complex and often dependent upon specific growth conditions.[42] Understanding how plants respond to changes in UV radiation against this backdrop of changes in multiple environmental variables is thus challenging but necessary in the context of future environments (e.g., Virjamo*, et al.* [43]). These UV-climate change interactions are particularly relevant for agroecosystems, where crop yield, food quality, pest and disease resistance and overall vulnerability to climate change can have significant impacts on food security (see section 3.5).

The effects of changes in incident solar UV radiation (UV-B and UV-A) on ecological communities and ecosystems are largely a consequence of impacts on primary producers (i.e, plants).[44-46] These higher-level ecological effects include changes in plant-plant interactions (competition), herbivory, pest-pathogen interactions and the decomposition of dead plant matter (litter) (see section 3.6). Although initially minor, some of these community and ecosystem effects may accumulate over time (e.g.,Robson*, et al.* [47]) or be amplified by processes such as competition.[48] For certain crop species, exposure to UV radiation can elicit changes in pest/pathogen defence that may have positive consequences for the productivity and sustainability of agroecosystems.[38, 45, 46]



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160 **Fig. 1.** Conceptual diagram illustrating known linkages between stratospheric ozone depletion, UV radiation
161 and climate change on terrestrial organisms and ecosystems. Stratospheric ozone depletion alters UV
162 radiation (primarily UV-B; arrow 1), which in turn directly affects plants and other organisms (arrow 2). The
163 effects on organisms can then alter the function and structure of ecosystems (arrow 3). Ozone depletion can
164 alter the climate, and climate change can affect ozone depletion via several avenues (arrow 4). Certain ozone-
165 depleting substances (e.g., hydrofluorocarbons (HFCs) and others) are potent greenhouse gases that can
166 enhance global warming. Stratospheric ozone depletion in the southern hemisphere is directly altering climate
167 via changes in the Southern Annular Mode (SAM) in addition to other climate changes. Resultant shifts in
168 climate zones alter regional rainfall and drought and thereby change cloud cover; in turn, the changing cloud
169 cover can increase or decrease exposures of organisms to UV radiation (arrow 5). Climate-related changes in
170 weather patterns (arrow 6) alter temperature and precipitation patterns, which can directly modify plant growth
171 and development, and the way in which plants respond to UV-B radiation (arrow 7). Climate change (including
172 altered UV-B exposure) is also changing the seasonal timing of development (e.g., phenology of flowering or
173 bud break; arrow 8), such that wild plants and crops develop at times of the year when UV radiation can be
174 either greater or less than prior to current rapid climate change (arrow 9). These phenological changes further
175 expose plants to novel combinations of UV radiation and other abiotic and biotic factors (arrow 10). In
176 response to climate change many organisms are shifting their ranges to higher elevations and latitudes (arrow
177 11). As with phenological shifts, these changes in geographic ranges can potentially increase (elevation) or
178 decrease (latitude) exposures to UV radiation (arrow 12), as well as subjecting organisms to new
179 combinations of UV radiation and other abiotic factors (arrow 13). As species migrate to different
180 environments they also encounter new combinations of competitors, pests and pollinators that may alter
181 important ecosystem processes such as herbivory and competition (arrow 14). Alterations in certain
182 ecosystem processes, such as decomposition, can modify soil carbon storage and emissions of carbon
183 dioxide and other greenhouse gases to the atmosphere (arrow 15). Image of stratospheric ozone shows total
184 ozone over Antarctica (October 2017, Source: https://ozonewatch.gsfc.nasa.gov/). Climate change map
185 indicates surface temperature anomalies for February 2017 compared to the base-period of 1951-1980
186 (Source: https://data.giss.nasa.gov/). Sonoran desert ecosystem photograph by P.W. Barnes.

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One important ecosystem-level effect of changes in UV radiation and climate is the altered decomposition of plant litter, which can result in a positive feedback to the climate system, thereby contributing to climate change. Photodegradation is the process whereby UV radiation, together with shorter wavelengths of visible radiation, drives the photochemical break-down of plant litter, and this results in the release of carbon dioxide and other gases to the atmosphere (Fig. 7).[49-51] Photodegradation can also modify the chemical make-up of litter, thereby promoting or facilitating the activities of microbial decomposers (bacteria and fungi; i.e., photo-facilitation). This results in increased microbial and soil respiration, and contributes additional carbon dioxide to the atmosphere.[52-54] At present, considerable uncertainty remains regarding the quantitative significance of photodegradation of terrestrial plant litter, and its effects on soil carbon storage and atmospheric carbon dioxide concentrations. However, it is clear that this process is an important driver of decomposition in many ecosystems, especially drylands (grasslands, deserts, and savannas).[54, 55] In some of these dryland ecosystems, the relative importance of UV-driven photodegradation may increase with climate change as precipitation decreases and temperature increases.[56] Changes in climate and land-use may also affect photodegradation and litter decomposition indirectly via changes in the structure and species composition of vegetation, and occurrence of fire and soil erosion (see section 3.6.3 and Sulzberger*, et al.* [51]).

There are several linkages between ozone depletion and climate change that are ecologically important but which do not directly involve changes in UV radiation. On the one hand, climate change can modify stratospheric ozone depletion by perturbing temperature dynamics between the stratosphere and troposphere.[57] Conversely, it is now apparent that ozone depletion in the southern hemisphere is directly contributing to climate change (Fig. 2).[4] Specifically, ozone depletion appears to be changing regional atmospheric circulation patterns in the southern hemisphere which, in turn, affect weather conditions, sea surface temperatures, and frequency of wildfires.[58-62] These changes together with changes in UV-B radiation can have several consequences for terrestrial ecosystems (see section 3.2, Fig. 3, and Table 1).[5] While ozone depletion in the northern hemisphere may be associated with similar, but smaller, climate shifts[4], to our knowledge there are no reports linking this to ecological impacts.

Finally, a better understanding of how terrestrial organisms and ecosystems might respond to changes in UV radiation in the context of modern climate change is coming from studies examining how plants and animals have adapted to changing UV radiation and climate conditions in the past. These historical studies, however, require some knowledge of how UV radiation has changed over geological time periods. In the absence of satellite or ground-based measurements of UV radiation, some investigators have attempted to reconstruct past UV radiation climates using biological

indicators as proxies for ground-level UV radiation. Section 3.8 evaluates progress made in the development of pollen grains and spores as bioindicators of past UV conditions.

3.2 Ecological impacts of ozone depletion-driven changes in climate in the southern hemisphere

Stratospheric ozone depletion has led to large changes in southern hemisphere climate (as detailed in Bais*, et al.* [4], Robinson and Erickson III [5], Bornman*, et al.* [8]). These are manifested in a mode of atmospheric variability, the Southern Annular Mode (SAM or Antarctic oscillation), which describes the difference in pressure between 60° and 45° S. The SAM describes the strength and latitudinal position of the westerly wind belt (i.e., jet stream) around Antarctica (see also, Robinson and Erickson III [5], Bornman*, et al.* [8]). Ozone depletion is linked to a highly positive phase of the SAM,[63, 64] corresponding to an increased pressure difference between mid- and high latitudes and a contraction of the westerly wind belt towards Antarctica (Fig. 2). The effects of this change in atmospheric circulation, which extend across the southern hemisphere, are summarised in the following sections. The sections emphasise how these changes in climate link to stratospheric ozone depletion (see also Bais*, et al.* [4]), affect abiotic drivers (e.g., wildfires) and the contingent responses of southern hemisphere ecosystems. The implications of these climate shifts for marine and aquatic ecosystems are described in Williamson*, et al.* [65]

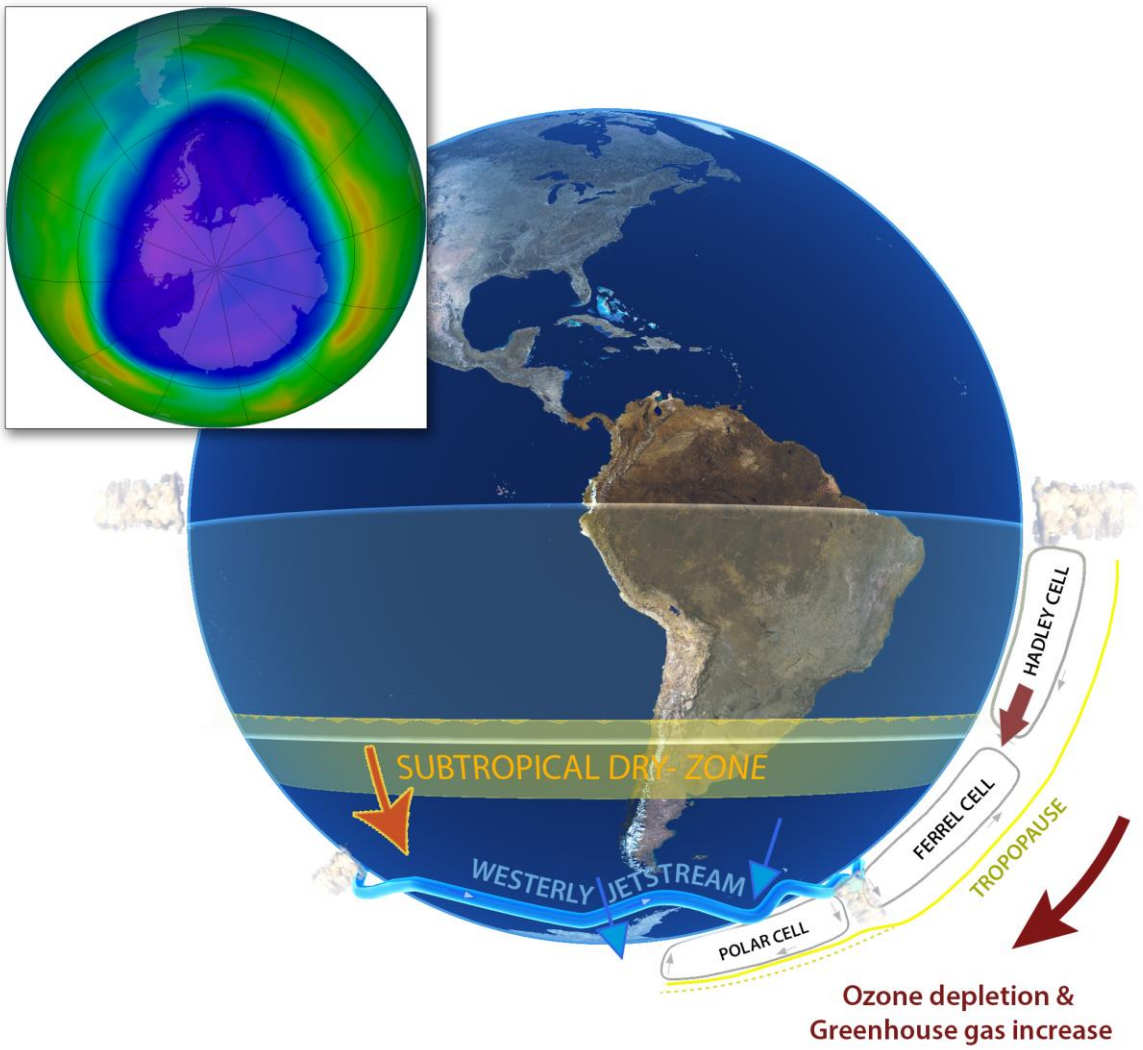

Fig. 2 The Antarctic ozone hole (inset) and its impact on southern hemisphere atmospheric circulation. Stratospheric ozone depletion and resultant cooling over Antarctica has caused the tropopause to lift, allowing the Hadley Cell (dark red arrow) and the westerly jet stream to tighten and shift towards the South (blue arrow). The speed of the jet has also increased (see Robinson and Erickson III [5] for details). The polar shift in the jet and its increased strength changes atmospheric and oceanic circulation throughout the southern hemisphere consistent with a more positive phase of the Southern Annular Mode (SAM; see text for explanation). Over the past century, increasing greenhouse gases and then ozone depletion over Antarctica have both pushed the SAM towards a more positive phase, and the SAM index is now at its highest level for at least 1000 years.[63] As a result, high latitude precipitation has increased and the mid-latitude dry zone has moved south (orange arrow). As the ozone layer recovers, increased greenhouse gas forcing will likely take over and the position of the jet is thus predicted to remain in this more southerly location. Figure adapted from Robinson and Erickson III [5] and Perlwitz [66], with ozone 'hole' over Antarctica, 17th September 2006, reproduced from NASA Ozone Watch.[67]

Changing concentrations of stratospheric ozone have been linked to changing surface temperatures, altered wind and ocean circulation patterns and changing precipitation patterns, causing increased rainfall or drought, the latter leading to increased risk of wildfires. As presented in our last assessment, terrestrial[8] and aquatic ecosystems[5] including biogeochemical cycling[68] have been affected by these changes across the southern hemisphere. Sections 3.2.1 and 3.2.2 give a

brief summary of the climate changes ascribed to ozone depletion and then address the implications of these changes for ecosystems in the southern hemisphere.

The UNEP Science Assessment Pane (SAP)[69] notes that since their last assessment,[70] further research has confirmed the impact of changes in stratospheric ozone on the tropospheric and surface climate of the southern hemisphere and has, in some cases, allowed better quantification and attribution of the changes. Stratospheric ozone depletion is assessed to have been the dominant driver of changes in atmospheric circulation across the southern hemisphere from the mid-latitudes to the tropics during austral summer (December-February) over the period 1960 to 2000 when stratospheric ozone was decreasing; while in other seasons, greenhouse gas emissions play a comparable role to stratospheric ozone depletion. As stratospheric ozone recovers, its effect on circulation should diminish; however, climate change is predicted to increasingly contribute to changes in atmospheric circulation.[4, 71, 72]

The major changes in mid-latitude and tropical circulations driven by stratospheric ozone depletion include the poleward shift of the mid-latitude jet (Fig. 2), the shift to an increasingly positive phase of the Southern Annular Mode (SAM) and the poleward shift of the sub-tropical Hadley Cell (Fig. 2).[39, 69, 73] Between 1980 and 2000, the westerly jet shifted south during summer by approximately one degree of latitude. Since 2000, the jet has shifted north in summer, although this reverse trend is not statistically significant.[69,74] A meta-analysis[75] supports stratospheric ozone depletion as the dominant driver of the Hadley Cell summertime expansion over the period 1979 to late 1990s.

3.2.1 Changes to southern hemisphere regional rainfall related to stratospheric ozone depletion, and ecosystem responses to fluctuating water availability: extreme rain, drought and fires

Changes in both extratropical and sub-tropical austral summer rainfall have previously been linked to the position of the mid-latitude jet and thus to stratospheric ozone depletion (Figs 2, 3).[4, 5, 8, 70, 76, 77] South-East South America (northern Argentina, Uruguay, southern Brazil and Paraguay) has experienced one of the largest increases in rainfall worldwide (Fig. 3; Table 1A)[78] with a 30% increase in summer rainfall over the past 50 to 100 years. While this increased rainfall appears to be the result of anthropogenic emissions of greenhouse gases,[79, 80] the relative contributions from greenhouse gases and ozone depletion to these changes have not yet been resolved (see also, Wu and Polvani [81,] Zhang*, et al.* [82]).

The SAM has been identified as the leading cause of changes in summer rainfall, surface temperature, and the diurnal temperature range in East Africa[83, 84], and these authors highlighted the

effects of stratospheric ozone depletion. Over the period 1961-1996, the position for the South Pacific Convergence Zone (a region of abundant precipitation, stretching from New Guinea towards southern hemisphere mid-latitudes) has changed, with increasing rainfall on the northern edge and decreases to the south.[85] This shift in precipitation appears related to stratospheric ozone concentrations, with models that isolate the impacts of ozone recovery suggesting a reversal of these effects as stratospheric ozone recovers. These shifts in rainfall patterns can have negative and positive effects on ecosystems, populations and individual species.

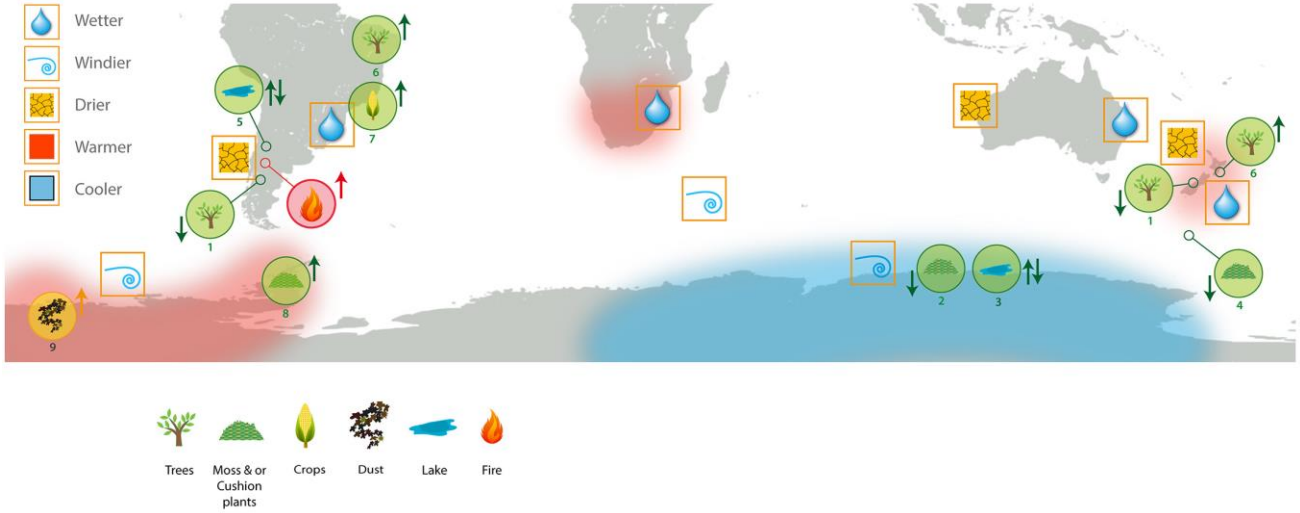

Fig. 3 Map of the southern hemisphere showing how stratospheric ozone depletion affects the climate and environment, and the effects of these abiotic changes on terrestrial ecosystems and populations. Symbols show types of organism, ecosystem or entity affected (see legend), with numbers referring to Table 1C, which provide species and location details. Arrows indicate direction of effects on biodiversity, up = positive, down = negative effects, two-way arrows indicate changed biodiversity.

317 **Table 1** Summary of how stratospheric ozone depletion affects the climate and environment (A) likely
318 consequences, (B) the effects of these abiotic changes on terrestrial ecosystems, and (C) populations across
319 the southern hemisphere. Regions affected and references are provided. Numbers (C) refer to locations in
320 Fig. 3.
321
322
323

A. **Changes in southern hemisphere climate driven by stratospheric ozone depletion**	**Regional examples**	**References**
Changing regional precipitation		4, 71, 86
Wetter	South East South America (Northern Argentina, Uruguay, southern Brazil and Paraguay)	78, 87
Wetter/Drier	New Guinea, southern hemisphere mid-latitudes wetter in the north and drier to the south Hydroclimatic variability over the Amazon Basin	85, 88
Drier	Chile, declining stream flows, consequences for ecosystem health and hydroelectric power	89
More extreme precipitation	South-eastern South America extreme Summer rainfall Heavy rain events in Madagascar	78, 81, 90-92
Changing ocean and atmospheric circulation		4, 71
Shifting location of wet and dry zones	Shifts in summer rainfall patterns, Australian summer - increased rainfall on mainland south east coast and decreased rainfall in western Tasmania. Sub-tropical dry zone also shifted towards the South Pole	83 93 73, 91, 94-96
Increasing surface wind-stress	Southern Ocean Leads to year-round stronger surface ocean warming Could enhance loss of Antarctic sea ice but see Bais, *et al.* [4] Alters mixed layer depth affecting nutrients	65, 97-99
Temperature		4, 71
Lower temperatures	Decrease in summer temperatures over East Antarctica, southeast and south-central Australia and inland areas of the tip of southern Africa. Eastern Tropical Pacific cooler	60, 96
Warmer temperatures	Much of Southern Africa warmer Warmer surface temperature and changed diurnal temperature range in East Africa Summer extreme temperatures, Australia, South America, Southern Africa	83, 96

324

B. **Likely indirect consequences of changes in southern hemisphere climate**	**Resulting from**	**References**
Changing cloud patterns	Latitudinal shifts in the Hadley and Polar Cells	94. See Bais, *et al.* [4] for

	mean that cloud cover has also shifted southward with ozone depletion	implications for exposure to UV radiation
Fire	Changes in precipitation can alter fire regimes; e.g., central and southern Chile	[51, 62, 100, 101]
Dissolved organic matter (DOM)	Changes in precipitation affect run off and quantity of DOM in water bodies	See Williamson, *et al.* [65] for details
Breakdown of litter	Changes in precipitation and temperature influence breakdown rates of litter	See Sulzberger, *et al.* [51] for details
Air quality	Weather [temperature, wind (transporting pollutants), rain and cloudiness] affects air quality with consequences for health of humans, other animals and plants	See Wilson, *et al.* [102] for details
Weathering of materials	Increased ambient temperature shortens the life of plastics and wood exposed to UV radiation, and their outdoor service lifetimes. Changing moisture also affects these processes	See Andrady, *et al.* [103] for modes of action

325

C. Drivers of change for terrestrial plants and ecosystems (number of marker on Fig. 3)	**Biological effects**	**Location**	**References**
Decreased water availability			
1	Less precipitation associated with decreasing growth of trees and restricted forest distribution	West New Zealand, South West S. America	[104, 105]
2 3	East Antarctic drying. **Moss beds** exhibit changing species composition. Reduced growth, more plant stress and death. **Lakes** are becoming more saline leading to biodiversity changes	Windmill Islands, East Antarctica	[106-108]
4	Drying caused more than 80% dieback of cushion plant and moss fellfield communities	Macquarie Island	[109]
Increased water availability			
5	Less salinity causes changes in lake fauna	Eastern side of the Andes	[110]
6	More precipitation associated with increasing growth of trees	East New Zealand, Eastern South America	[104]
7	Expansion of agricultural zones with more precipitation	South East S. America	[111 78]
8	Moss beds and other biodiversity more productive due to warmer wetter conditions and more land	Antarctic Peninsula	[112-114]
Increased wind speeds			
9	Risk of increased dust and potential propagule inputs into Antarctica (negative if introduces non-native species)	West Antarctic, Antarctic Peninsula	[115-118]

Ecosystem responses to fluctuating water availability. Shifting atmospheric circulation cells (Hadley, Ferrel and Polar cells, see Fig. 2) alter regional precipitation across the southern hemisphere, causing some areas to receive more moisture and others to become drier. In Patagonia, declines in tree growth have been linked to reduced water availability (Fig. 3; Table 1B).[104] In the extreme south of South America extending into Antarctica, lichens are an increasingly-dominant component of the terrestrial biota.[119] Lichens are extremely tolerant of desiccation, but nevertheless the combination of high wind speeds and high irradiance, including increased UV-B radiation due to ozone depletion, have been shown to affect their colonisation on trees in Patagonia.[120] However, lichens grow very slowly,[121] so responses to specific climatic changes can take a long time to detect. Less seasonal precipitation and a reduced diurnal temperature range were the dominant factors driving aridity and limiting the distribution of high-elevation woodlands of *Polylepis tarapacana* (a rose family tree species of high conservation value, found in the South American Altiplano). Models predict that by the end of this century almost half of the potential habitat of this species will be lost due to increased aridity.[105]

Decreased precipitation in this region of South America has led to reduced stream flows in Chile, with adverse effects on aquatic and terrestrial ecosystems as well as the production of hydroelectric power.[89] Since the 1960s, warming and associated drying at mid- and high-latitudes to the west of the Andes have resulted in increased forest fires (measured from fire scars in tree ring records).[62] During the 2016–2017 fire season, more than 500,000 hectares burned in central and southern Chile (between ~29°S and 40°S), driven by a long-lasting drought linked to the positive SAM that was amplified by El Niño–Southern Oscillation (ENSO) conditions. Given that the positive phase of SAM is predicted to continue, it is likely that increased wildfire activity in southern South America will continue throughout the 21st century.[62]

Several other regions of the southern hemisphere have experienced wetter summers[4], leading to increased tree growth in eastern New Zealand[104] and expansion of agriculture in south-eastern South America (Fig. 3; Table 1B).[78] The eastern side of the Andes has experienced wetter conditions with associated biodiversity changes. For example, changes in fauna (ostracods and chironomids) from lake sediments in El Toro Lake (40˚S, 70˚W) indicate that the lake has become fresher (less salty) as a result of increased precipitation since the middle of the 20th century, associated with the positive phase of SAM.[110]

Increasing extremes of precipitation have also been linked to SAM-related changes. Rainfall patterns in the southern Amazon Basin have been reconstructed from tree rings of *Centrolobium*

362 *microchaete*[88] and the findings suggest that the fluctuations between drought and extremely wet
363 seasons seen from 1950 to the present day may be unmatched since 1799.
364
365 **3.2.2 Changes in surface temperatures as a consequence of stratospheric ozone depletion**
366 **and implications for terrestrial ecosystems**
367
368 Recent studies[122, 123] suggest that warming of West Antarctica and the Antarctic Peninsula may fall
369 within the range of natural climate variability.[124] This warming had previously been linked to
370 anthropogenic emissions of greenhouse gases and stratospheric ozone depletion.[5, 8] Stratospheric
371 ozone depletion could account for between a quarter and one third of summer and autumn cooling
372 over the rest of the Antarctic continent (see Robinson and Erickson III [5]). However, our confidence in
373 any attribution or projections of climate warming over this region is limited by the large biases
374 inherent in the models used. Depletion of Antarctic stratospheric ozone over Antarctica has possibly
375 offset a substantial portion of the summer warming that would otherwise have occurred (due to
376 increasing greenhouse gases) in eastern Australia, southern Africa and South America (Fig. 3).[96]
377 These changes in temperature are likely to have affected (positively and negatively) life cycles of
378 plants and animals, potentially leading to mismatches between plants and their pollinators (see
379 section 3.7.3). Cooler temperatures over East Antarctica have likely slowed the melting of ice
380 sheets. As stratospheric ozone concentrations recover, the extent of this amelioration may be
381 reduced with potential implications for the climate and populations of these regions as well as further
382 afield.
383
384 In western Antarctica, along the Antarctic Peninsula and on nearby islands, increasing
385 temperatures[60] were associated with increased productivity of terrestrial ecosystems (microbial
386 productivity, plant growth rates and carbon accumulation in moss beds) from the 1950s to the turn of
387 the century.[114] There is some evidence that the direction of these changes has reversed since 2000,
388 consistent with recent cooling in this region.[114,125,126] However, as noted above, the relative
389 contributions of stratospheric ozone depletion *vs* increasing greenhouse gases to temperature
390 changes is still unresolved because recent studies suggest they are not beyond the range of natural
391 variability (see above and Bais*, et al.* [4]).
392
393 On the opposite side of the continent, in the Windmill Islands of East Antarctica, decreased water
394 availability since the 1960s, linked to decreasing temperatures and increasing wind,[107] has resulted
395 in changes in biodiversity in both Antarctic moss beds[106] and lakes,[108] with species composition
396 changing to reflect the newly drier moss beds and more saline lakes. In addition, these East
397 Antarctic plant communities are becoming more stressed as a result of drying, resulting in
398 increasingly moribund moss.[106, 127, 128] This is one of the first studies[106] to document ecosystem-level

399 changes in Antarctic terrestrial plant communities, which are correlated with the SAM and potentially
400 linked to stratospheric ozone depletion and climate change. Further north, widespread (>80%)
401 dieback of cushion plants (*Azorella macquariensis*) and mosses, on sub-Antarctic, Macquarie
402 Island, was primarily attributed to reduced water availability as a result of higher wind speeds, more
403 sunshine hours and therefore higher evapotranspiration since the 1970s. The authors estimate that
404 from 1992 to 2008 these plant communities suffered accumulated water deficit for 17 years.[109] This
405 dieback of Antarctic and sub-Antarctic vegetation is similar to the "*Arctic browning"* observed in the
406 Arctic in response to extreme climate events.[129, 130]
407
408 ***Interannual variability.*** Two studies have linked interannual variability of springtime Antarctic
409 ozone to summer changes in surface temperature and rainfall in the southern hemisphere.[96, 131] The
410 SAP 2018 report[69] concludes that interannual variability in springtime ozone at both Poles may be
411 important for surface climate, but the extent of this connection is not fully understood.
412
413 Stratospheric ozone-driven climate change has widespread and far-reaching effects on terrestrial
414 and marine ecosystems (see Williamson*, et al.* [65]) across the southern hemisphere. A better
415 understanding is needed of the relative contributions of stratospheric ozone, greenhouse gases and
416 interannual variability in order to determine the ecological or biological change attributable to
417 stratospheric ozone depletion *vs* that due to these other climate factors. Nevertheless, we have
418 only included studies in this section where a strong signal of ozone depletion or summer SAM has
419 been associated with an ecological effect.
420
421 ## 3.3 Plant response to UV radiation and interactions with climate change
422 ## factors
423
424 There is now a basic understanding of UV-sensing and UV-signaling in plants, as well as the
425 consequences for gene-expression, physiology, biochemistry, plant growth, fitness and nutritional
426 quality. Potentially, UV-B radiation can damage plants through effects on DNA, the photosynthetic
427 machinery, and other cellular targets. However, UV-B-induced plant defence responses, including
428 up-regulation of photorepair processes, antioxidant capacity, and UV-screening, are thought to be
429 effective in the prevention of damage to plants by UV-B radiation under most natural conditions.
430 Nevertheless, effective prevention and repair do not imply that UV radiation has no effect on plants.
431 Acclimation to UV radiation and climate change factors can modify plant growth and development,
432 which, in turn, has consequences for ecosystem functioning (section 3.6), nutritional quality and
433 food security (section 3.5). Thus, understanding plant response to UV radiation and some of the
434 interactive effects of climate, is of fundamental importance for evaluating effects of UV-B radiation
435 on terrestrial ecosystems.

3.3.1 Limitations to current studies investigating interactive effects

Much of our understanding of plant responses to UV radiation began with single-factor experiments in laboratories, greenhouses, and controlled environment chambers that did not account for interactive effects from multiple climate factors. Overall there is evidence that conditions in artificial environments may unrealistically accentuate the negative effects of UV-B radiation on plant growth. For instance, such studies are often conducted in growth chambers or greenhouses where lamps are used as the principle source of UV-B radiation and the ratio of UV-B radiation to photosynthetically active radiation (PAR, 400-700 nm) is far above that generally found in field conditions. We illustrate these limitations for some recent controlled-environment studies (Fig. 4). Note that only 16 of the 49 studies surveyed provided sufficient UV and PAR data to be represented as data points in the figure.

It is important to use the knowledge from these studies to design experiments for testing the results at more expansive scales of space and time. Laboratory results may be scaled up by progressively moving to more realistic conditions in controlled environments and then to field experiments (e.g., Flint and Caldwell [132]). Another scaling approach is to design experiments moving from our common organism-centered methodology to a community or ecosystem perspective, where interactions, feedbacks, and their relative magnitudes under realistic conditions are examined.[133] Some recent studies have investigated the effects of UV-B radiation in combination with other climate change factors, such as drought, temperature, carbon dioxide, and tropospheric ozone (e.g., Martinez-Luscher*, et al.* [134], Wijewardana*, et al.* [135], Mao*, et al.* [136]). For this assessment we evaluated the experimental studies and methodological protocols,[137] resulting in the exclusion of some studies in our summary findings.

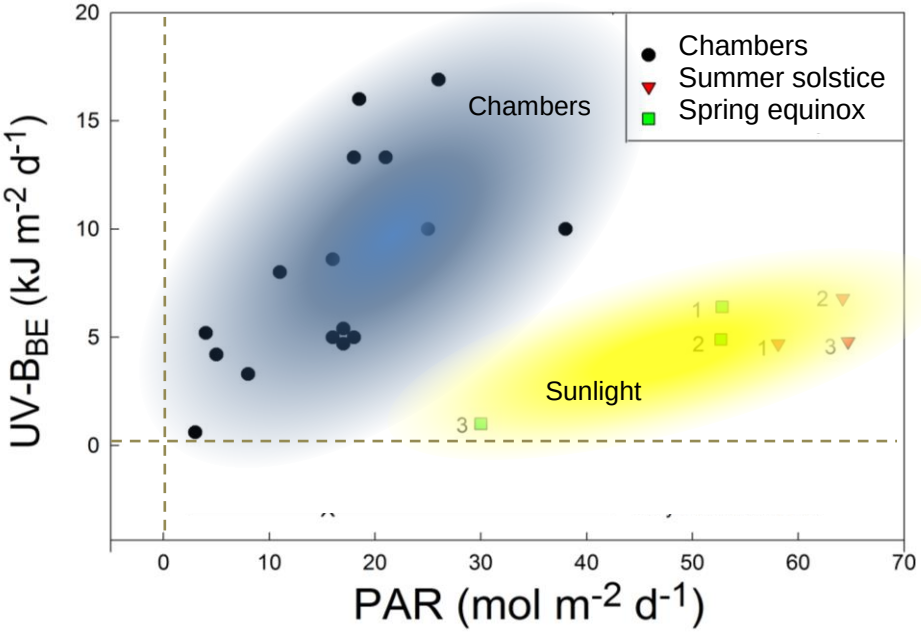

Fig. 4 Studies conducted in growth chambers (blue) are still using unrealistic ratios of photosynthetically active radiation (PAR, 400-700 nm) to biologically effective UV-B radiation (UV-B_{BE}; data were reported using the generalized plant action spectrum of Caldwell [138] (more commonly used in these studies than the action spectrum of Flint and Caldwell [139]) compared with natural sunlight (yellow). Growth chamber experiments are represented by black circles within the blue shading. Solar irradiances within the yellow shading represent the summer solstice (red triangles) and spring equinox (green squares). Ambient PAR is from Ritchie [140] and ambient UV-B_{BE} was computed with the TUV calculator: http://cprm.acom.ucar.edu/Models/TUV/Interactive_TUV/. Latitudinal locations are indicated by numerals: 1. Equator (0°), 2. Tropic of Cancer (23°N), and 3. 55°N. A total of 49 peer-reviewed papers on growth chamber studies from the years 2011-2017 were surveyed; 16 are represented as data points in this figure and 33 could not be represented, because they either lacked radiation data or it was not measured in a manner comparable to the other studies.

3.3.2 The UV-B photoreceptor and signaling pathways

The existence and nature of a specific UV-B photoreceptor in plants, the protein, UVR8, initially came to light in 2011.[141] Since this discovery, a basic understanding of UV-sensing, signaling and function has emerged that has improved our knowledge of the molecular mechanisms underlying UV defence and acclimation in plants.[22, 34, 141]

UVR8-mediated perception of UV-B radiation contributes to up-regulation of the expression of genes that encode components of the phenylpropanoid biosynthesis pathway, photorepair of DNA damage, and enhanced antioxidant capacity.[22] Penetration of UV-B radiation into leaves depends on the concentration of flavonoids and other phenolics in the epidermis, as well as plant anatomical and morphological characteristics that vary among species. Most of the UV-B radiation is strongly attenuated as it passes through the epidermis, although it has been measured in some herbaceous plant species in deeper-lying tissues (mesophyll layers), with 18-41% epidermal transmittance.[142, 143] Given that the UVR8 protein has been detected in most plant tissues investigated, including roots, it is currently difficult to pinpoint in which plant tissues perception of UV-B radiation takes place in plants growing in sunlight. Tissue-specific analysis of UVR8 activity has revealed that the UV-B-induced UVR8 signalling pathway in epidermal and mesophyll cells is involved in hypocotyl elongation, while UVR8 expression in the epidermis contributes to cotyledon expansion.[144] Thus, the UV-B-induced response appears to be partly mediated by tissue-autonomous signaling, although inter-tissue signaling may also be involved.[144] The role of UVR8 is not simply limited to protection from UV-B radiation. There is now strong evidence that UVR8-mediated signaling extends to processes such as stomatal function, de-etiolation (greening response of plants), entrainment (alignment with) the circadian clock, phototropism, and defence against pathogens.[34] These findings, mainly on the model plant, *Arabidopsis thaliana* (a type of cress), provide a frame of reference for the study of the multifaceted role of UV-B perception through photoreceptor(s) in the regulation of plant growth and development in the much more complex natural environment. This

frame of reference can also be used for other plant species that are likely to follow a variety of strategies to acclimate and adapt to their habitats.

While much attention has been given to elucidating UVR8-mediated processes, UVR8 is not the only UV-B sensing mechanism in plants. There are also UVR8-independent signaling pathways,[145] for example, arising from oxidative stress and via UV-B-mediated DNA damage,[146] including generation of cyclobutane pyrimidine dimers (CPD, one of the main types of DNA damage). However, CPD photolyase, which repairs the damage, is predominantly regulated in a UVR8-dependent manner in plants exposed to UV-B radiation. There is evidence that the UVR8-mediated signaling pathway regulates the scavenging capacity of reactive oxygen species (ROS),[147] and the production of nitric oxide in response to UV-B-induced stress.[148] These latter molecules may themselves play a role in signaling.[148]

Thus, plant responses to UV-B radiation likely involve multiple UV signaling pathways. Moreover, components of these UV-mediated signaling pathways interact with other stress-induced signaling pathways, such as those activated by other wavelengths of light, exposure to drought, extreme temperatures, and other factors associated with climate change.

3.3.3 UV-B-mediated signaling, crosstalk and cross-tolerance

There is still a lack of information and understanding concerning the effects of UV-B radiation in a complex environment where plants are simultaneously or sequentially exposed to multiple environmental factors that can modify plant growth and development.

In principle, the simultaneous application of treatments involving changes in two environmental factors can lead to additive, synergistic, antagonistic or no effect. It is particularly relevant from an agronomic perspective that acclimation responses induced by changes in one environmental factor can confer cross-tolerance (including priming responses) or cross-sensitivity to another factor. Exchange of information between distinct plant-signalling pathways can broaden the spectrum of responses to one particular environmental factor. For example, high levels of PAR and UV-B radiation generally increase the accumulation of flavonoids, with synergistic effects occurring in some cases when plants are exposed to a combination of both variables.[149, 150] Such increases of protective pigments with antioxidant activity potentially enhance the tolerance of a plant to a variety of unfavourable conditions.

Cross-talk also occurs when UV-B-mediated signalling cascades interact with signalling pathways induced by biotic variables, e.g., bacteria. This cross-talk can sometimes lead to a shift in other plant

defences at the expense of the UV-induction of protective mechanisms, such as the accumulation of flavonoids.[151] In this case, the UV-B-induced genes of the flavonoid pathway are suppressed by the bacterial elicitor, flg22 (a peptide), which in turn drives the immune response against the bacterium[152] by stimulating pathogen-protective compounds called phytoalexins. In other cases, UV-B radiation can increase plant resistance against pathogens and pests, by increasing the accumulation of metabolites involved in plant defence against multiple stress factors (reviewed in Ballaré[153]). Other examples of cross-talk where UV-B radiation is implicated in plant stress responses include changes in some plant hormones, such as auxin, cytokinin, gibberellic acid, brassinosteroids and jasmonic acid.[154-156] UV-cross-talk involving the hormone abscisic acid can result in increased plant tolerance to water stress, extreme temperatures, or salinity. Some of these aspects are evaluated in the next section.

The interactions between UV-signalling and other signalling pathways imply that subtle molecular effects of UV-B radiation may potentially extend to many aspects of growth and development, with implications for ecosystems including agricultural systems under conditions of current and future climate change.

3.3.4 Plant and ecosystem response to potential interactive effects of UV-B radiation and climate change factors

Exposure to changing environmental conditions can directly affect plant growth and may also drive changes in phenology (section 3.7.3) and shifts in the distribution ranges of species (section 3.7.1). Here we will specifically explore interactions between UV-B radiation and certain key abiotic climate variables. In comparison to studies on interactive effects of UV-B radiation and drought and/or temperature, far less is known about interactive effects of UV-B radiation and elevated CO_2 on plants.

UV radiation and drought. The potential for plant responses to UV radiation and drought to be complementary has been the subject of research because seasonal droughts are usually coincident with, or follow, periods of prolonged sunny weather, implying high exposure to UV radiation. An example of such synergies comes from an experiment with silver birch (*Betula pendula* L.) seedlings subjected to treatments combining solar UV-B radiation and water stress outdoors in southern Finland. In this investigation, leaf and whole plant water potential responded to the combination of ambient UV-B radiation, conferring resistance to drought, which was visible through reduced wilting and lower mortality beyond that of UV-B radiation or water stress alone.[41] Plant responses to the combinations of UV-B radiation and drought should be considered when selecting agricultural crops, as plant responses to these factors can have consequences for crop quality.[157]

Additional research provides evidence for synergies in response to drought and UV-B radiation.[158, 159] However, both the mechanisms and outcome of response to combinations of water stress and UV-B radiation are often inconsistent. To some extent, the seemingly contradictory results reflect differences among studies in the timing and levels of drought and UV-B radiation applied to the plants. Sequential exposure to two environmental variables can allow the first to elicit a response that primes the plant for the second, resulting in cross-protection. In contrast, simultaneous exposure may weaken plant defences.[160] In this context, it should be noted that few, if any existing studies have adequately reproduced natural combinations of exposure to UV-B radiation and drought as well as their relative timing, and therefore results from these studies need to be carefully evaluated for their relevance (see Fig. 4).

Reduced cloudiness is expected to lead to increases in UV-B radiation and future seasonal droughts in Mediterranean ecosystems.[161, 162] A study, where solar UV radiation was filtered in a Mediterranean ecosystem under normal and reduced rainfall, showed plants to be tolerant of UV-B radiation independently of the rainfall regime and seasonal climatic conditions. In this case, the species tested were evergreen Mediterranean shrubs with tough thick leaves high in phenolics.[163] Thus, life history, together with exposure protocols, choice of species and dose-dependency will all determine the outcome of the interactive effects of drought and UV-B radiation.

Perhaps the most important complication in attempting to understand the interactive effects of drought and UV-B radiation, is that both variables alone induce complex responses, and any simultaneous exposure to both variables will result in an amplification of that complexity. Cross-protection is multifaceted and likely to involve decreases in leaf area and possibly stomatal gas exchange, increases in leaf and cuticle thickness, as well as enhanced concentrations of antioxidants, flavonoids and potentially a range of other secondary metabolites such as proline and volatile terpenes.[164] Osmotic stress-induced upregulation of the UVR8 transcript and protein levels might also contribute to interactive effects of drought and UV-B radiation.[165] This complexity can also be observed in a study where, only in the presence of ambient UV radiation did drought increase canopy temperature and result in decreased accumulation of above-ground biomass in a grassland ecosystem..[166] Thus, interactive effects of drought and UV-B radiation need to be considered in the context of prevailing and future conditions, particularly warming temperatures.

UV radiation and temperature. On balance, rising average air temperatures associated with climate change are expected to affect the growth and survival of many plant and animal species, and perturb many ecosystem processes. In addition to changes in average temperatures, extremes in temperature have increased in frequency and magnitude,[167] which can have severe local and

regional consequences. Changes in seasonal weather patterns and sky conditions are bringing periods of high temperatures, which are often accompanied by high solar radiation including UV-B radiation to many regions. However, extreme cold temperatures can also be accompanied by high UV-B radiation, particularly at high elevations and latitudes in springtime where UV-B radiation reflected by the snowpack[168] often supplements the irradiance received by organisms exposed to the sun.[169] The combinations of UV-B radiation and temperature can affect plant acclimation processes (see below), which are important in terms of understanding the response of ecosystems to climate change, how future agroecosystems will be managed, as well as how vegetation itself affects air quality and climate.[102]

Exposure to high UV-B radiation and elevated temperatures elicits a variety of chemical responses in plants. For example, UV-B radiation can induce production of volatile hydrocarbons, such as the isoprenes,[170] and this has been associated with heat tolerance mediated by membrane stabilisation. Typically, isoprene emission occurs in woody plants, contributing to air pollution and global carbon. Global annual emissions of isoprene are estimated to be equivalent to 300 Tg carbon yr^{-1} (=300 x 10^{12} g C yr^{-1}) with changes depending on climate change and land-use.[171] Isoprenes, as well as other plant-produced biogenic volatile organic compounds such as monoterpenes, have an important effect on atmospheric composition, and ultimately climate. Exposure to elevated temperature combined with UV-B radiation can cause more isoprenes to be emitted than under elevated temperature alone, as was found for European aspen.[172] UV-induced isoprene production is synergistically enhanced in response to higher temperatures, and this has significant implications for both plant thermotolerance and plant-herbivore interactions.[173]

An outdoor field experiment in Finland found that UV-B radiation enhanced accumulation of condensed tannins in aspen, but this increase was negated by 2°C above ambient temperature treatment in the spring and summer.[174] This process may directly impinge on herbivory, given that tannins act as defence compounds that inhibit digestion (also see section 3.6). In willow, the same combination of UV-B radiation and temperature produced a similar pattern of effects on the accumulation of phenolic compounds.[175]

It is well known that both the total content and composition of flavonoid compounds in plant leaves can be modified by a number of environmental factors including UV radiation, and high and low temperatures.[176-180] For example, kale (*Brassica oleracea* var. *sabellica*) exposed to a low temperature of 5˚C accumulates almost twice as much of the polyphenol, kaempferol-3-O-sophoroside-7-O-glucoside, as plants at 15˚C. Such stimulatory effects may also completely mask UV-B-induced accumulation of flavonoids, as was seen in an outdoor study where plants under low temperatures accumulated high concentrations of UV-screening pigments, and this response was

unaffected by the UV-exposure regime.[180] However, the profile (or composition) of the polyphenols is also modified, whereby kale plants at 15˚C accumulate *ca* 25% more kaempferol-3-O-caffeoyl-sophoroside-7-O-glucoside but 30% less kaempferol-3-O-sophoroside-7-O-glucoside.[178] At present, the function of these changes in phenolic profiles are not clear, although some of the compositional changes result in compounds with higher antioxidant activity. Since flavonoids are considered desirable by the food and nutrition industries (see also sections 3.5.2 and 3.5.3), an understanding is needed of changing phenolic profiles under different environmental conditions.

3.4 Perception of and response to UV radiation in animals

UV-B radiation has the potential to damage tissues in animals, but many animals, like humans,[181] have mechanisms that protect against the potentially deleterious effects of UV-B radiation. Nonetheless, there are reported cases of UV-induced injury in animals (see section 3.4.1; and Bornman*, et al.* [8]). Apart from UV damage, many animals perceive UV radiation and can use these cues to lessen exposure to intense UV radiation. Also, some animals use UV radiation as a source of information for mate selection, foraging, predator avoidance, and other behaviours. Traditionally, an anthropocentric or human-centric perspective has resulted in a narrow definition of "visible light," appropriate only for human vision. However, it has long been known that many species have vision that encompasses different wavelengths of the spectrum, sometimes including the UV region. Animals known to have UV vision include species of insects, amphibians, reptiles, birds and mammals.[21] While advances have been made in understanding the mechanism of UV vision in animals, it is unclear how changes in the UV environment, as a consequence of changes in stratospheric ozone and climate change, might alter the UV sensory responses of these organisms (section 3.4.2).

3.4.1 UV radiation damage to animals

Ultraviolet-B radiation is known to be potentially deleterious to a wide variety of terrestrial animals. Under controlled conditions, it has been shown that UV-A and UV-B radiation can damage the skin and eyes of various amphibian species (e.g., newts, frogs, bullfrogs, treefrogs), with the potential to negatively affect their foraging ability and fitness (reviewed by Blaustein and Kats [182,] Bancroft*, et al.* [183]). For example, in South America there are indications that land-use and climate change may lead to increased exposure to UV radiation in the habitats of frog species, e.g., *Hypsiboas curupi* and *Hypsiboas pulchellus.*[184-186] However, while UV radiation may impair vision and cause DNA damage to frogs, it is not considered at present to be among the most important environmental factors contributing to the reduced fitness and abundance of several frog species in this region.[187]

3.4.2 UV vision in animals and ecological implications in changing environments

The eyes of insects and mites have specific rhodopsin photoreceptors that perceive UV radiation,[188] which may be important in avoiding excessive UV radiation.[20] In other insects, such as damselflies, UV-reflecting wings appear to play a direct role in mate recognition by creating visual signals of sex and age.[189]

Birds have UV-A vision and photoreceptor UVS-cones (sensitive to wavelengths longer than 355 nm), which may assist in foraging and mate choice.[21] For instance, woodpeckers use visual cues in the UV-A region to forage on decaying wood, which differs in UV-absorption according to the extent of its fungal colonisation. Changes in the amount of UV radiation in the environment (e.g., due to changing weather patterns or forest cover) may affect visibility of these fungi and hence alter the behaviour of woodpeckers foraging for them. Changes in mutualisms of this sort have broad consequences for ecosystem function.[190] In other birds, UV-absorbing melanin in their feathers has been linked with sexual selection but also UV-protection and thermoregulation, and UV protection over wide geographic gradients.[191] Many bird species display strong sexual differentiation (dichromatism), creating specific patterns through both melanin accumulation and UV-reflectance of feathers.[192] UV patterning[193], including UV-absorbance and reflectance, are not limited to feathers and their putative role in mate selection, but are also used in a much broader range of visual recognition processes. For example, UV-reflection of bird eggs attracts aerial predators.[193, 194] Conversely, UV-absorbing melanin in egg shells may protect eggs from UV-B radiation directly and reduce their visibility to predators, although the dark pigmented colour may cause overheating in some environments. Across a variety of species, including a palmate newt (*Lissotriton helveticus*), the expression of SWS1 opsin, a UV-photoreceptor in the eyes of animals, is UV-dependent[195, 196]; furthermore, plasticity in expression of the photoreceptor depends on the habitat of population origin. This suggests that changes in the amount of UV radiation in the environment during the development of these newts could affect visual sensitivity in the UV region.[197, 198]

The role of UV-B radiation has been relatively well-studied in the case of lizards. Lizards kept in captivity are routinely exposed to low background levels of UV-B radiation to enhance vitamin D synthesis and their overall health.[199] UV-reflectance of lateral blue spots in male lizards has a clear role in male-male interactions, including the processes of mutual assessment.[200] If two males have an equal signal from their UV-reflecting throat patch, their behaviour towards each other is more aggressive.[201]

At present, evidence for an ecological role of UV vision in animals is steadily increasing, but detailed information of the functional role of UV-absorbing or reflecting tissues often remains a matter of

speculation. There is also a lack of information on the dose-response of UV-visual recognition processes. Thus, it is not known how changes in stratospheric ozone and climate change-driven alterations in exposures to UV radiation will influence visual cues in animals or whether altitudinal or latitudinal gradients in UV radiation might affect migration or range shifts in these animals. Nevertheless, understanding of UV vision in animals is of direct relevance in the context of food security and specifically plant-pest and plant-pollinator interactions.

3.5 Food security and agricultural ecosystems

At mid-latitudes and the tropics, there are indications of recovery of ozone in the upper stratosphere. However, the total ozone column, which is the metric of greatest relevance for terrestrial ecosystems, has not yet started to recover. Because of increasing concentrations of greenhouse gases, the total ozone column over mid-latitudes will be larger by the second half of the 21st century compared to the time prior to the release of the ozone depleting substances into the atmosphere. Changes in total ozone over the tropics will be relatively small and will depend on emission scenarios and climate change-related phenomena.[4, 39] Nevertheless, the relatively high levels of UV radiation that occur in the tropics and at high elevations, together with ozone-independent, location-specific factors such as decreasing concentrations of aerosols, less cloud cover and changes in land-use,[4] mean that crops may still be subject to significant changes in exposure to UV radiation. Some areas will also receive less UV radiation where pollution levels continue to be high, including increasing frequencies of smoke from forest fires.[65] These levels of complexity can affect agroecosystems with respect to growth, development and survival. It is in this context that crop plant and agricultural responses to UV radiation and climate change will be assessed here. Particular attention is given to plant defence mechanisms, implications of genotype, and crop quality mediated through changes in plant biochemistry.

3.5.1 Linking UV radiation and climate effects to food security

The interactive effects of UV radiation, climate change, and changes in land-use and management practices, are likely to have consequences for agriculture and food security. For example, these factors can modify crop yield and quality, pest and disease resistance and overall vulnerability or adaptation to the environmental changes (Fig. 5). From the human intervention perspective, clearing of land for increased agricultural production to cope with growing populations, leads not only to increased exposure of agroecosystems to UV radiation, but also to poorer quality soils and soil erosion. In areas receiving increased UV radiation, plants may more readily express acclimative mechanisms against disease, herbivores, and other environmental stresses. Farmers and growers

are also becoming increasingly interested in the advantage of UV-induced stimulation of desirable secondary metabolites, such as the polyphenolics, in order to achieve improved crop response to stress conditions, including drought, pests and diseases.[45, 202-206]

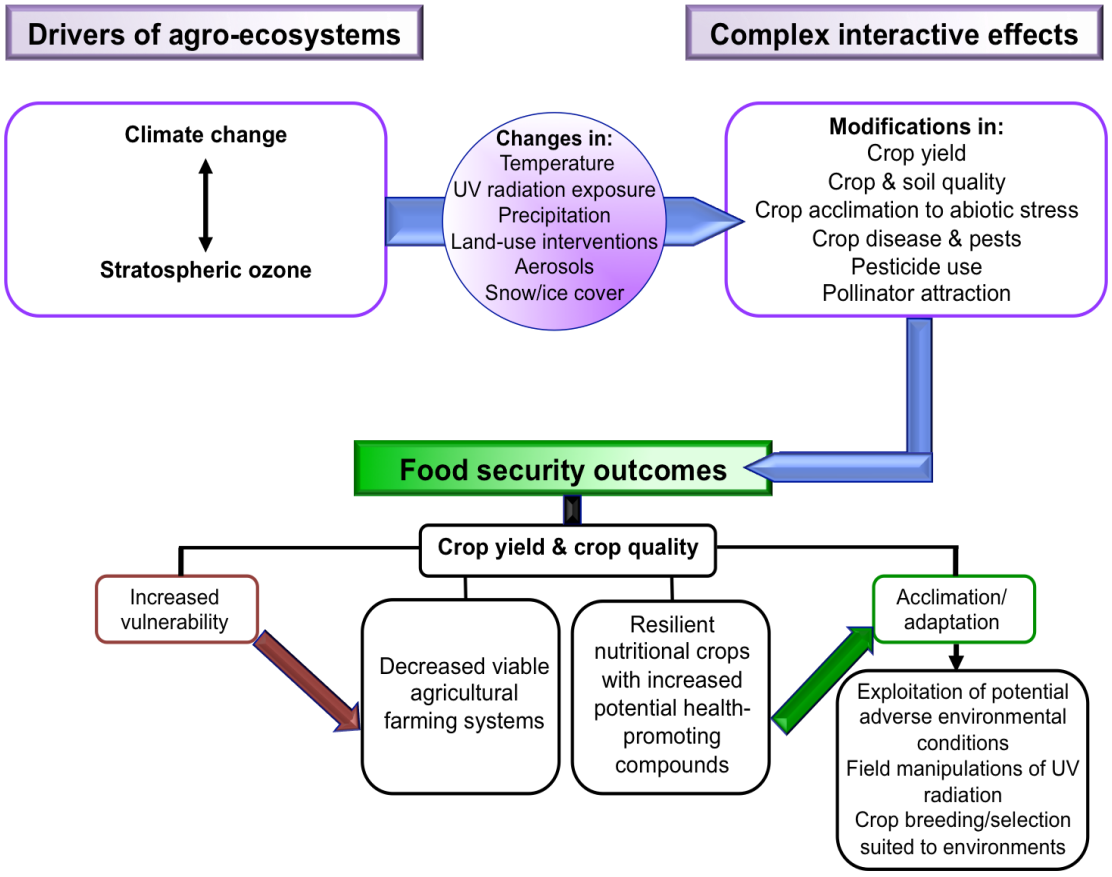

Fig. 5 Examples of current and evolving drivers of change on food security, showing the effects of linkages between changes in stratospheric ozone and climate.

3.5.2 Effect of genotype and environment on crop yield and quality

The degree of plant acclimation to stress conditions is often dependent on cultivar or genotype,[177, 207, 208] as well as location and growth conditions.[177, 209-211] Environmental conditions and genotype have been shown to be key factors that determine crop plant response and yield, and are indicative of the general phenotypic plasticity of plants (changes in morphological, physiological and metabolic attributes). The roles of both the environment and genotype are especially important when assessing current and future plant acclimation to stressful environments, including locations exposed to high levels of UV-B radiation, low rainfall and extremes of temperature (e.g., Andean Altiplano and Tibetan Plateaux). Thus, research investigating the 'environment x genotype' response of crop plants is important for selection of genotypes suitable to particular environments and levels of UV-B radiation. The composition, concentration and antioxidant activity of polyphenolics change according to plant exposure to elevated UV-B radiation and vary strongly with

plant genotype.[177, 212] The selection of responsive genotypes or cultivars can be used to improve the nutritional status of a crop, because of the potential benefits of antioxidants (conferring free radical scavenging capability) and other plant components.[213] These benefits may include the potential for reducing the risk of health-related diseases such as cardiovascular disease and Type 2 diabetes.[214-216]

3.5.3 Importance of secondary metabolites in agro-ecosystems

Ultraviolet-B radiation regulates the accumulation of numerous secondary metabolites, including flavonoids and other compounds derived from the phenylpropanoid pathway. These metabolites are important for plant growth and development, as antioxidants, UV-screening pigments, herbivore and pathogen deterrents, as well as serving as pollinator attractants and improving nutritional quality,[217, 218] flavour, visual appeal and desirability of many foods.[8,45,219 and references therein,220-224] However, exposure to UV-B radiation may cause both desirable and less desirable changes in nutritive properties. For example, UV-B radiation can decrease protein content in some crops or increase essential fatty acids not synthesised by humans and other animals (i.e., polyunsaturated linoleic and linolenic acids), while decreasing other beneficial fatty acids, such as the monounsaturated oleic acid, as was found in a study on soybean seeds.[225]

The UV-B-induced regulation of phenolic compounds can occur under low levels of UV-B radiation in many plant species, including in a range of economically important crops in which these metabolites contribute to food quality and/or value. For instance, UV-B radiation mediates increased accumulation of the potentially nutritionally-valuable flavonoid compounds, quercetin and kaempferol, in grape berry skins.[226] The phenolic composition of grape berry skins can also change along latitudinal gradients. This was shown in a study where these flavonoid compounds were favoured in the south compared with the north (from 36.7°N Jerez, Spain to 50°N Geisenheim, Germany), a change which positively correlated with overall solar radiation across multiple European sites.[227] This finding suggests that field manipulation of the exposure of grapes to UV-B radiation and other fruit crops could be exploited to enhance desirable characteristics. Such field manipulations are already in development.[45, 228-230]

Although UV-B radiation can affect food quality, this does not only involve phenolics, but a much broader range of metabolite classes including UV-regulated terpenoids, aromatic esters and others.[231] In peaches exposed to UV-B radiation, levels of the flavour-related monoterpene, linalool, decrease, while concentrations of sesquiterpene (E,E)-α-farnesene increase.[170] Volatile isoprenes have also been associated with thermotolerance (see section 3.3.4). Specific glucosinolate compounds may also accumulate in plants exposed to UV-B radiation,[232] and may lead to the

production of certain defence compounds against herbivory, creating another link with observations of reduced herbivory in plants exposed to UV-B radiation (see section 3.6.2), although the degree of resistance to herbivory under UV-B radiation may also be dependent on the type of herbivore.([173]; and section 3.5.4)

Decreases in UV-B radiation in southern South America and Australasia as the stratospheric ozone layer recovers[4], may have negative effects for plants and agricultural crops in some cases. For example, as noted above, since UV radiation generally enhances production of plant secondary metabolites that deter many plant herbivores[173], a decreased induction of these polyphenolics may result in increased herbivory and plant disease. It follows that from an environmental and food safety perspective, reduced cross-protection against herbivores, resulting from decreased UV-induced accumulation of phenolic compounds in crop plants under projected lower future UV-B radiation exposures, may result in increased pesticide use.[38] There is also evidence that UV radiation can promote the breakdown of certain pesticides (e.g., fenitrothion[233], triazophos[234, 235]).

3.5.4 Potential effect of UV radiation on the visibility of crops to insect pests and pollinators

As well as being herbivores, insect pests are the main carriers of plant viruses, which are a major cause of plant disease and restrict yields through decreased plant vigour.[236] In agricultural and horticultural environments, reductions in UV radiation, whether through climate change (e.g., cloudiness, aerosols, forest fires) or deliberate intervention (e.g., the use of UV-attenuating screens, plastic films or nets), can reduce visibility of crops for some insect pests. However, certain pests, such as whitefly, aphids and thrips may be more damaging to crops in environments with UV radiation compared with environments where UV radiation has been attenuated or reflected,[236, 237], although exceptions have been reported.[7, 238] On the other hand, some beneficial insects such as pollinators, are more effective in environments containing UV radiation, allowing them to use floral cues such as UV-absorbing/reflecting nectar guides (reviewed by Llorens*, et al.* [239]). The floral patterns produced by nectar guides can be species-specific as found in the genus *Potentilla* where flowers of species from different regions of its distribution appear similar in the visible spectrum but differ in their UV nectar guides, presumably as an adaptation to attract different pollinators (Fig. 6).

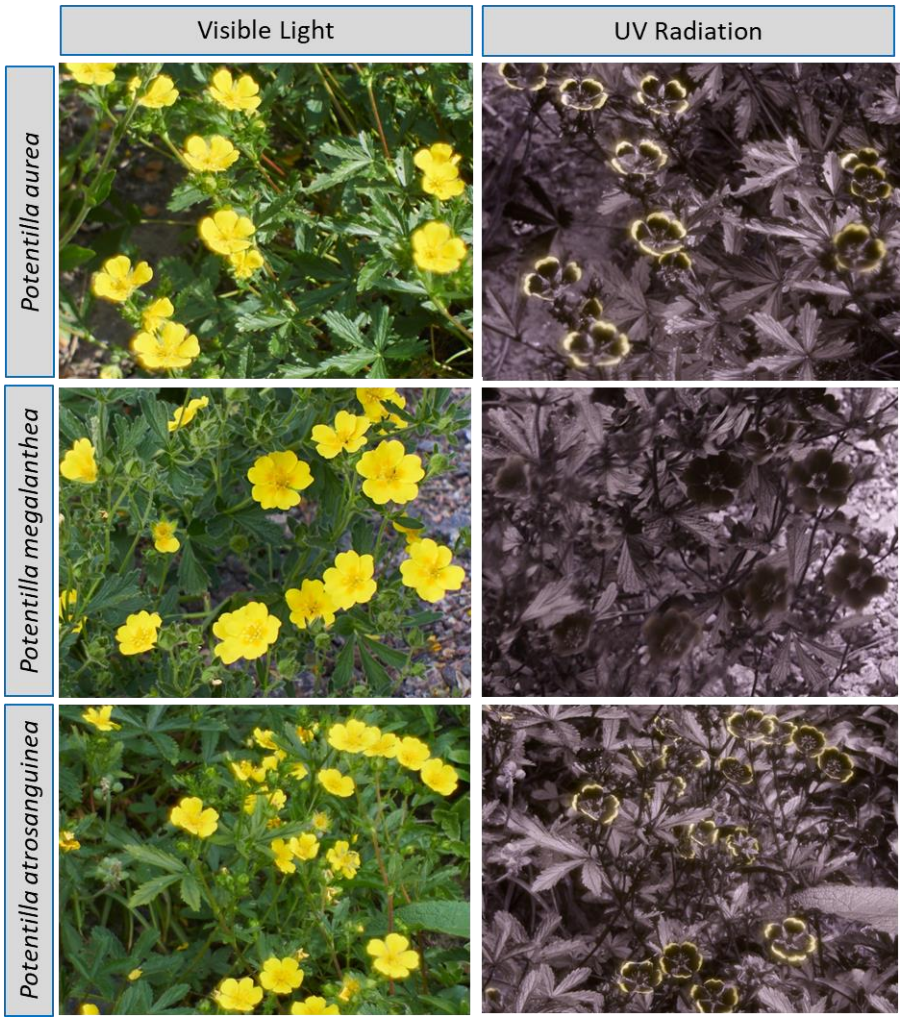

Fig. 6 The three *Potentilla* species with different origins growing together in Helsinki Finland: *Potentilla atrosanguinea var. argyrophylla* (Himalayan cinquefoil) originates at high elevations; *Potentilla megalanthea* is from Japan; and *Potentilla aurea* is European. While looking similar in the visible spectrum their flowers have very different UV-absorbing and reflecting nectar guides that are visible to insect pollinators. UV photographs were taken with a filter blocking visible radiation but transmitting in the UV-A as far as 325 nm. Photographs by T.M. Robson and P.J. Aphalo.

These effects of UV radiation on insects have implications for crop yields and the use of agrochemicals to control pests. However, in controlled environments growers must balance the benefits of UV radiation for plants providing higher food quality[240, 241] against any potential costs in terms of the visibility of the plants to pests such as fruit flies (*Drosophila suzukii*[235]) thrips and aphids.[206, 242]

Thus, the interplay of changing levels of UV-B radiation and increased frequency of extreme weather events is likely to add to the current and projected vulnerability of agriculture with consequences for food security (Fig. 5). The key climate drivers together with UV-B radiation that modify plant development and yield are usually temperature and water availability.[243-245]

Consequently, the capacity of plant acclimative mechanisms to adjust to the rapidly changing conditions will become increasingly important.

3.6 Ecosystem functioning

Terrestrial ecosystems can be modified in several ways by the interactive effects of ozone depletion, UV radiation and climate change. Below, we consider recent findings that address the impacts of these interactions between plants (plant-plant), plant-herbivore, pest-pathogen, and litter decomposition. Some of these processes, particularly litter decomposition, are important in biogeochemical cycles. The consequences of alterations in these ecosystem processes for nutrient cycling and climate change are addressed more fully by Sulzberger*, et al.* [51].

3.6.1 Plant-plant interactions

Plants interact with one another in positive (facilitation) and negative (competition) ways and these interactions can ultimately change the composition of plant communities and their development following disturbance (succession). Competition between crops and weeds is also an important process affecting agricultural productivity and can require considerable labour and economic investment in weed control. Past studies have shown that enhanced UV-B radiation can shift the balance of competition between crop and weed species, and that these changes are linked to differential effects of UV-B radiation on plant morphology, which then alters competition for light within plant canopies (reviewed in Barnes*, et al.* [48]). Similarly, exposure to ambient UV-B radiation has been shown to change species composition in alpine plant communities, and these changes were also associated with differential effects of UV-B radiation on plant height and leaf area.[246] Modelling studies confirm that these differential effects of UV-B radiation on plant growth and morphology can lead to shifts in competitive relationships among species.[247] At least some modifications to shoot morphology are likely mediated by the UV-B photoreceptor, UVR8.[22, 141] Plants appear to use UVR8, along with other photoreceptor proteins (e.g., phytochromes), to sense changes in the light environment caused by the proximity of other plants.[248, 249] Low light conditions (shade) inactivate UVR8, which then results in plant resources being redirected from defence to rapid growth.[249] However, while this strategy helps the plant to compete for light with its neighbours, it also makes it more vulnerable to the attack of pathogens and pests (reviewed in Ballaré [153], Ballaré and Pierik [250]; see section 3.6.2 below).

3.6.2 Herbivory and plant-pathogen interactions

Plant responses to UV-B radiation have consequences for organisms at various trophic levels or positions along the ecological food chain from producer to consumer. Solar UV-B radiation-induced reductions in herbivory have been well-documented in the field, and when this occurs, may be proportionally much larger than the effects of UV-B radiation on inhibiting plant growth (reviewed in Ballaré*, et al.* [7]). However, there are also instances where herbivory increases with UV-B radiation (see section 3.5.4). Herbivorous insects can perceive solar UV-B radiation,[251] although many of the inhibitory effects of UV-B radiation on insect herbivory and pathogens are thought to be indirect (i.e., mediated by changes in host-plant chemistry; reviewed in Ballaré[153]). More limited evidence indicates that solar UV-B radiation can reduce infection by some plant pathogens. This increased pathogen resistance was shown in experiments where plants were pretreated with different amounts of UV-B radiation before inoculation with a pathogen.[252]

Shade-intolerant plants often down-regulate or decrease their defences against pathogens and pests in those leaves that are exposed to shade or shade signals (such as a low red to far-red ratio, R:FR),[253-256] presumably allowing for resources to be redirected into growth responses to avoid shade. According to this interpretation, plants growing in patchy canopies use solar UV-B radiation as a "gap" signal to adaptively regulate their growth and defence phenotypes. The interplay between shade signals (such as low R:FR perceived by phytochromes) and gap signals (such as high levels of UV-B radiation) may optimise the allocation of resources between growth and defence (see Demkura*, et al.* [257] and reviews of Ballaré [153,] and Mazza and Ballaré [249]).

Some of the changes in plant chemistry elicited by natural levels of solar UV-B radiation involve compounds known to be important for plant interactions with other organisms (reviewed in Escobar-Bravo*, et al.* [173,] and Williamson*, et al.* [258]). Known defence-related compounds regulated by UV-B radiation include phenylpropanoid compounds,[259] isoflavonoids,[260, 261] conjugated polyamines,[257] cuticular waxes,[262] proteinase inhibitors,[263, 264] and jasmonates,[265] among others. These effects of solar UV-B radiation on defensive chemistry can be considered as specific, presumably mediated by specific UV-B photoreceptors. However, the role of UVR8 in mediating effects of UV-B radiation on secondary compounds has so far been demonstrated only for flavonoids and other soluble phenolic compounds.[252, 266]

In spite of the effects of UV-B radiation on plant defence against several herbivores and certain pathogens, the connections between UV-B radiation and the key hormonal pathways that regulate plant defence (i.e., the salicylic acid (SA) and jasmonic acid (JA) pathways), require further research. Early reports of effects of UV radiation on SA and expression of SA marker genes should be interpreted cautiously, as many of those experiments used doses or wavelengths of UV radiation not present in the terrestrial environment (such as UV-C, <280 nm), or unbalanced UV-B radiation

968 treatments (high UV-B radiation delivered against low PAR; see Fig. 4). Similar limitations apply to
969 early studies of effects of UV radiation on JA activity (reviewed in Ballaré [153]).
970
971 Some well-characterised effects of UV-B radiation on plant defence come from experiments that
972 tested plant resistance to herbivorous insects, and necrotrophic pathogens (pathogens that kill their
973 host cells). This has led to follow-up work focusing on interactions with JA signaling. A few studies
974 have shown that genetic perturbations impairing JA synthesis can effectively cancel out some anti-
975 herbivore effects of solar UV-B radiation, leading to the suggestion that JA signaling is required for
976 those effects of solar UV-B radiation that increase plant resistance to herbivory.[257, 267, 268] However,
977 UV-B radiation can also affect plant defence against herbivores and pathogens via mechanisms that
978 are not mediated by JA.[252] The positive effects of UV-B radiation on JA signaling have been
979 attributed to increased JA biosynthesis[265] or sensitivity,[257] but the molecular mechanisms linking
980 perception of UV-B radiation and JA signaling remain to be elucidated.
981
982 **3.6.3 Litter decomposition**
983
984 The decomposition of dead plant material (i.e., litter) drives the rate at which nutrients are recycled
985 and is a strong determinant of carbon storage and soil fertility in terrestrial ecosystems. In general,
986 the overall rate of decomposition is dependent on the temperature and moisture availability, which
987 affects the activity of decomposing micro-organisms (bacteria and fungi), as well as the type of plant
988 litter inputs (e.g., leaf *vs* woody tissue; evergreen *vs* deciduous leaves). Substantial evidence now
989 indicates that solar radiation (UV and short wavelength visible radiation) can also drive litter
990 decomposition via several mechanisms, with the net effect of these processes either accelerating or
991 retarding decomposition, depending on litter quality and environmental conditions. Climate change
992 will likely alter the importance that UV radiation plays in decomposition and regulating carbon
993 cycling in a number of terrestrial ecosystems.
994
995 Solar radiation in the UV and short-wavelength visible regions (blue and green light) can directly
996 break down the biochemical components of plant tissue, including relatively stable compounds, such
997 as lignin, which absorb UV radiation, through a process called photochemical mineralisation (Fig. 7;
998 [46, 269, 270]. These light-driven modifications in litter chemistry can, in turn, increase the ease with
999 which microbes can decompose litter.[52, 54] This latter process is often called photo-facilitation or
1000 photopriming. However, solar UV radiation, especially shorter wavelength UV-B radiation, may also
1001 inhibit the activity of microbes and change the composition of the microbial community, which then
1002 works in opposition to photo-facilitation.[270, 271] The net effect of these mechanisms is modified by

environmental conditions (e.g., moisture availability) and the spectral quality of sunlight, which varies depending on ozone depletion, cloud cover, pollution, and plant canopy cover.

Recent studies have shown that photodegradation (photochemical mineralisation plus photo-facilitation) occurs in a variety of environments,[54] but the mechanisms and quantitative importance of this process in driving the overall decomposition of litter remains unclear in many cases. Since UV radiation can also inhibit microbial activity, a shift in spectral composition (i.e., UV-B:PAR ratios) would likely change the balance between photo-facilitation and microbial inhibition. This may be one reason why some experimental and modelling studies fail to detect a relationship between photodegradation and lignin content of litter.[55, 271] Long-term studies indicate that increased rates of decomposition due to photodegradation become evident only in later stages of decomposition, as was found after 4 months for savanna litter in a controlled experiment,[272] and after 12 months in a semi-arid ecosystem.[273] This suggests that the availability of substrates to microbes is only noticeably increased by photo-facilitation once readily-available substrates in fresh litter have been depleted. A diel time period (i.e., 24 h) appears to allow microbes to benefit from daytime photo-facilitation, possibly recovering during darkness, as well as utilising the extra humidity at night.[272, 274]

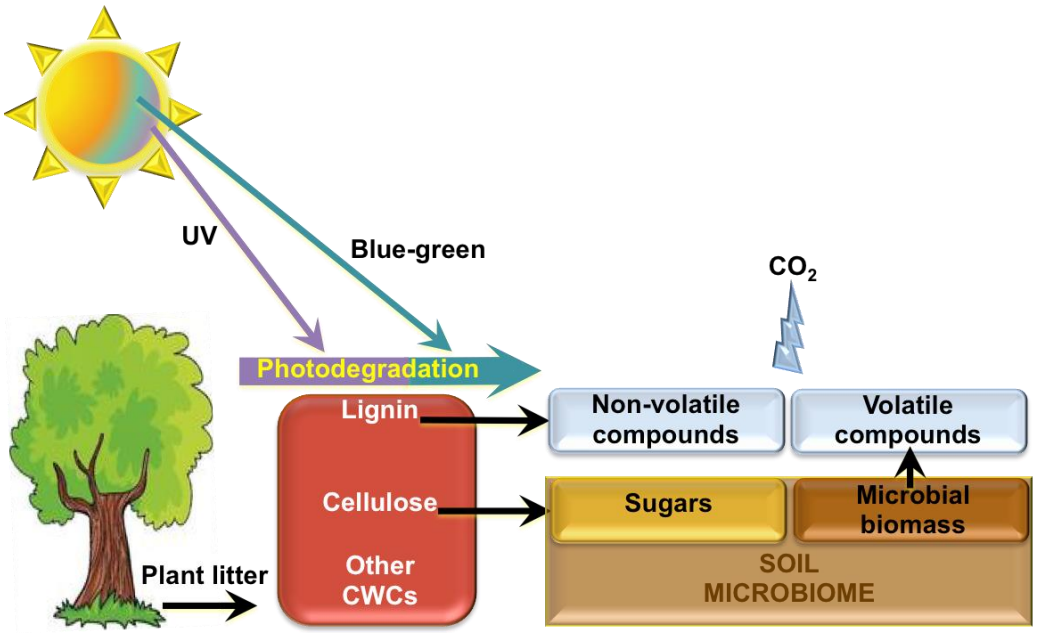

Fig. 7 Conceptual model of the effects of solar radiation on litter degradation and microbial decomposition in terrestrial ecosystems. UV radiation and blue-green light cause the direct breakdown of lignin, cellulose and other plant cell wall components (CWCs), forming non-volatile and volatile compounds, such as carbon dioxide (CO_2), the latter being released to the atmosphere. This abiotic process is often referred to as photomineralisation. The changes in litter substrate resulting from photodegradation enhance the microbial breakdown of litter through a process called photo-facilitation. UV photons in sunlight may also directly inhibit the activity of decomposing microbes. Figure adapted from Ballaré and Austin [46].

Field studies continue to show that photodegradation contributes most to the acceleration of litter decomposition in hyper-arid (annual precipitation <150 mm), arid, and semi-arid eco-systems.[275, 276] In two contrasting locations on the Mediterranean steppe, UV radiation increased the decomposition rate of grass and shrub litter in a continental climate, but not in a high rainfall maritime climate.[274, 277] These findings suggest that in drylands photochemical mineralisation dominates under the driest conditions, whereas photo-facilitation tends to dominate under slightly moister conditions. The acceleration of decomposition attributable to photo-facilitation can even be detected in sub-tropical and temperate environments in both litter and coarse woody debris.[278] However, when moisture levels are favourable enough to support high microbial activity, UV radiation can have negative effects on decomposition, presumably because of direct inhibitory effects of solar radiation on the microbial populations.[279]

The majority of field photodegradation studies to date have been conducted in ecosystems occurring in dry (arid and semi-arid) rather than moist (mesic) climates.[270] However, the interaction of moisture and photodegradation has recently been garnering attention.[274, 276, 280] In moist, forested ecosystems, the amount of solar radiation reaching litter through the canopy can alter decomposition rates.[281] Different types and densities of canopy affect both the amount of radiation reaching ground level and its spectral composition.[282] This implies that shifts in vegetation type occurring because of changes in land-use and climate are likely to affect decomposition rates through photodegradation interacting with concomitant changes in temperature and moisture.[283-285] Typically, the encroachment of woody plants leading to conversion of grasslands to shrublands driven by climate change and/or land abandonment, will alter litter composition and chemistry. This will shift litter C:N ratios, affecting not only microbial activity but also photo-facilitation of litter and direct photodegradation.[283, 286, 287] In addition to shifts in vegetation type, the exposure of litter to solar radiation will be determined by plant form and functional strategy. In habitats where standing dead litter remains on the plant, this will present a greater surface area exposed to sunlight than situations where litter falls to the ground becoming easily mixed with soil which then reduces photodegradation.[273, 276, 288-290]

The structure and biochemical composition of litter produced by different plant forms plays a significant role in determining the underlying rate of decomposition. Hence litter with high lignin content may decompose slowly and be most affected by direct photochemical degradation.[68, 291] However, variations in photodegradation among species independently of their lignin content,[269] suggest that other litter traits are also important (see Bais*, et al.* [39] for additional discussion). The UV radiation received by plants during growth can affect leaf morphology and the amount and composition of phenolic compounds that accumulate in the leaf epidermis,[8] as well as affecting the rate at which leaves will break down. These traits may continue to modify leaf optical properties and

hence the extent to which solar radiation penetrates the leaf during the early stages of decomposition.[292] Likewise, the depth and density of litter, its physical movement (e.g., by wind, rain) and the degree to which litter mixes with soil, will determine the surface area exposed to sunlight, factors that are likely to be highly important for photodegradation.[269, 270]

The insight that recent research brings into the role of both UV radiation and short-wavelength visible light in photodegradation in humid temperate as well as arid biomes,[56, 293] means that photodegradation has the potential to modify ecosystem processes (e.g., carbon cycling) across many biomes. This broader relevance compared with our past knowledge of photodegradation extends its scope to affect the biogeochemistry of terrestrial ecosystems under climate change and with future stratospheric ozone recovery.[51]

3.7 Climate change is altering the exposure of organisms to UV radiation

Previous assessments have focused on the effects of ozone-driven changes in UV-B radiation.[8] However, climate change is increasingly exerting a stronger control on UV-B and UV-A radiation received by organisms as a result of changing cloud cover, vegetative cover, shifting of geographic ranges of species, changing of seasonal timing of growth and reproduction, and migration. Some of the potential implications of these climate-driven changes in exposure to UV radiation for terrestrial organisms and ecosystems are addressed below.

3.7.1 Species migration, UV radiation and climate change

Plants and animals are shifting their ranges to higher latitudes and elevations in response to climate change and additional changes in distributions are expected to occur in the future.[1, 2, 294] However, species vary in their potential rates of migration. For plants, short-lived, herbaceous species (grasses and forbs) generally shift geographic ranges more rapidly than long-lived, woody species (trees and shrubs).[1] Non-native (i.e., introduced) species of plants also appear to exhibit higher migration potentials than native (i.e., indigenous) species.[294, 295] These climate change-driven shifts in geographic ranges will likely alter the exposure of plants to UV-B radiation, since UV-B irradiances generally increase with increasing elevation and decrease with increasing latitude[16, 17, 161]. However, these changes in plant exposure to UV-B radiation will not occur in isolation of other environmental factors, since a number of abiotic (e.g., temperature and moisture) and biotic (e.g., associated pests, pathogens and competitors) factors change with the migration of organisms to higher latitude and elevation.[1, 296] Consequently, these shifts in geographical range will likely expose organisms to unique combinations of UV radiation and co-occurring environmental factors. To what extent UV radiation plays a role in influencing migration patterns and how plants and

animals respond to different conditions of UV radiation in the context of these other environmental changes as they migrate, has received little attention to date (but see section 3.3). However, certain insights into these effects can be gleaned from studies comparing plant populations or ecotypes whose distribution naturally spans a range of latitudes or elevations.

Plants that are adapted to grow in high elevation environments (i.e., alpine) often accumulate more UV-screening compounds (e.g., flavonoids) and have other UV-protective mechanisms compared with those plants occurring at lower elevations.[297-301] These differences are likely the result of the combined effects of elevational changes in UV radiation, temperature and other factors.[302] As discussed in section 3.3.4, **l**ow temperatures induce the production and accumulation of flavonoids. This may then increase levels of UV-screening and protection against oxidative stress.[303-305] High- and low-elevation plant populations may also differ their abilities to acclimate to changes in UV radiation.[306] In wild potatoes (*Solanum kurtzianum*), populations grown at low elevation have relatively low constitutive (base-line) levels of leaf flavonoids but a high capacity for induction of flavonoids when UV radiation increases. In contrast, plants at high elevations have high constitutive flavonoid levels, but do not necessarily increase their UV-screening in response to supplemental UV-B radiation in experimental studies.[307] Differential sensitivity to UV radiation of high *vs* low-elevation populations may also be due, in part, to population differences in DNA damage and repair, as has been shown for *Arabidopsis.*[306]

Whether there are differences in tolerance to UV radiation between native *vs* introduced species is unclear at present. For example, introduced populations of Chinese tallow tree (*Triadaca sebifera*), taken from south-eastern USA where the species was introduced in the 1700's, were shown to be more sensitive to UV-B radiation than native Chinese populations.[308] By comparison, no differences were found in the sensitivity of seed germination to UV-B radiation in native *vs* introduced populations of *Verbascum* and *Echium* in New Zealand.[309] Similarly, native and non-native species showed similar levels of UV-screening when growing in a high UV, tropical alpine location.[310] However, UV-screening increased with increasing elevation and UV-B radiation in a non-native species (*Verbascum thapsus* (mullein)) but did not vary with elevation in the native *Vaccinium reticulatum* (`ohelo). In contrast, similar levels of phenotypic plasticity (acclimation potential) between native (German) and non-native (New Zealand) populations of *Hieracium pilosella* with respect to morphological and growth response to UV-B radiation under growth chamber conditions have been found.[311] Thus, while it is generally assumed that non-native species can acclimate more readily to environmental change than native species,[312] it is unclear whether this generalisation applies to tolerance to UV-B radiation. Plants expanding their distribution into higher latitudes, would be expected to experience less exposure to UV-B radiation. As already noted, this may then lead to

a decline in UV-screening compounds, antioxidants and other metabolites involved in photo-protection.[313]

To date, relatively little research has exploited remote sensing to make quantitative assessments of plant responses to elevation and climate change. However, the potential to use this approach is apparent from remote sensing images of a 1-hectare area (from the Carnegie Airborne Observatory-2), using a high-fidelity visible-to-shortwave infrared (VSWIR) imaging spectrometer and dual laser waveform (LiDAR), which was calibrated against spectrophotometric measurements of leaf extracts.[314] This allowed a trend to be identified for increased phenolics with elevation (excluding the upper-most measurement point) using LiDAR images at the landscape scale in the Peruvian Andean rainforest. As this approach becomes more widely adopted, it will enable the resolution of large-scale relationships with topography and climate, allowing patterns in response to UV radiation and climate change to be mapped using remote sensing of large areas. Unmanned aerial vehicles (drones) are also increasingly being used to bridge the gap between satellites and ground measurements and to measure spectral reflectance at high resolution and under clouds.[127]

Ecosystems, and populations of plant species, including native species, have responded over the eons to changing environmental conditions. However, the recent rapid rate of climate change, in particular increasing temperatures and more frequent extreme weather events, are of concern in terms of the conservation of species and habitats.[2] Understanding the role of UV radiation in shifting distribution patterns and how readily plant populations can adjust physiologically and genetically to new UV radiation environments is therefore relevant to the conservation of biodiversity and the services that these natural ecosystems provide to humans.

3.7.2 Clouds, canopies and plant response to fluctuating UV radiation conditions

Climate change is altering cloud cover with some regions experiencing increased and other regions decreased cloud cover.[1, 4] The effect of clouds on UV radiation also depends on the type of clouds [315] as well as their position relative to the sun.[316] These changes in cloud cover alter the long-term (days to weeks) exposure of plants to UV radiation and they can also change the short-term (seconds to hours) dynamics of UV radiation received by plants. (Fig. 8; [316]) Whereas considerable attention has been given to understanding plant responses to changes in average UV radiation conditions that occur over long time periods (section 3.3; see also Bornman*, et al.* [8,] and Björn [24] and references therein), far less is known about plant responses to rapid fluctuations in solar UV radiation. A number of studies have, however, demonstrated that UV-screening levels in mature leaves can vary over the growing season[317], from one day to the next,[318] over the course of an individual day,[319] and in response to rapid changes in clouds.[320] The changes in UV-screening that

occur over the day are rapid (within minutes), reversible, and have been shown to be linked to changes in the content and composition of UV-absorbing compounds (flavonoids and related phenolics).[319, 320] At present, the underlying mechanisms responsible for these rapid changes in UV-radiation protection are unclear, as is the significance of these changes for plant growth and function. These findings do, however, indicate that many, but not all, plant species can rapidly adjust their UV-screening in response to fluctuations in UV irradiances.[321]

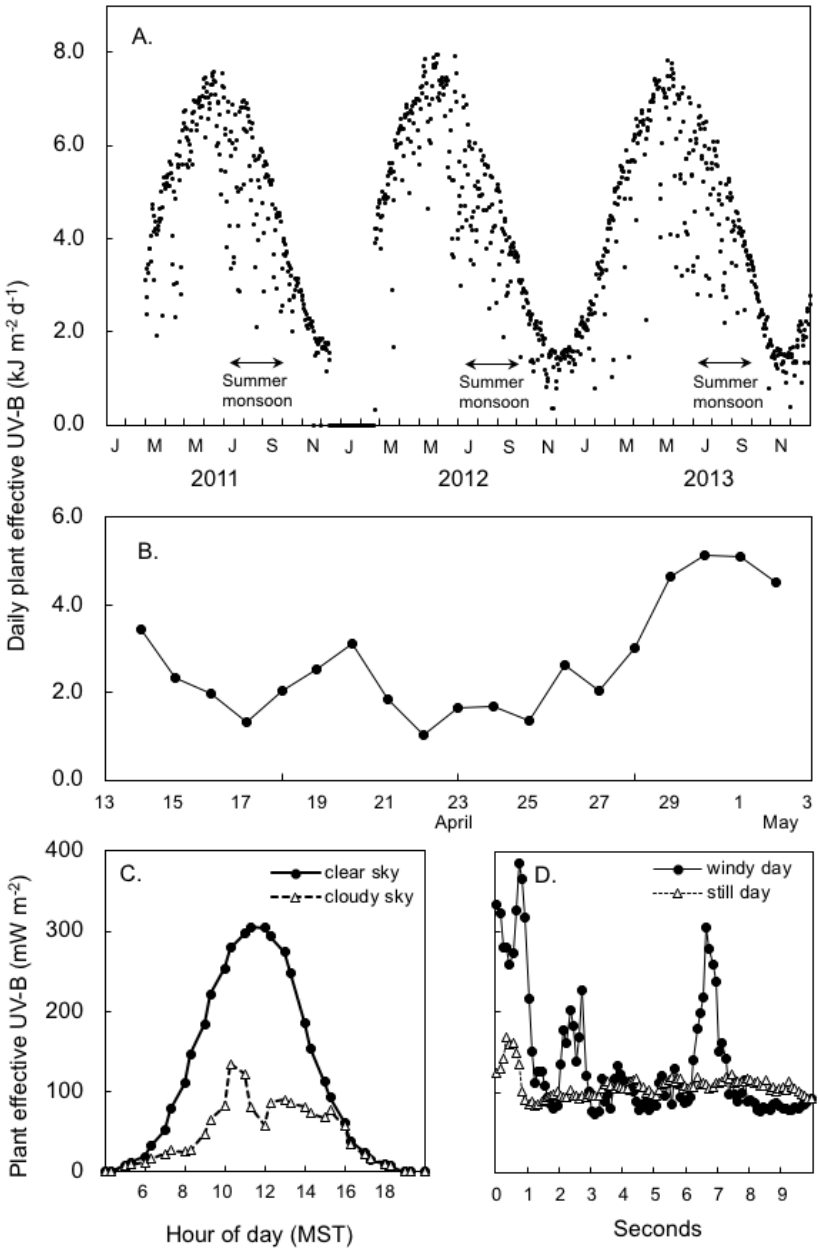

Fig. 8 Variability in ground-level UV-B radiation at several locations over multiple time scales. Panel A shows incident daily plant effective UV-B radiation in the Sonoran Desert, USA, over a 3-year period with annual summer monsoon (rainy and cloudy weather) indicated. Panel B: daily plant effective UV-B radiation in eastern Washington, USA, over an early spring period with heavy cloud cover followed by clear skies during a time when the new leaves of many native plant species are emerging. Panel C: diurnal changes in plant effective UV-B radiation under summer clear and cloudy skies in the Sonoran Desert. Panel D: changes in instantaneous plant effective UV-B radiation in an understory location of a birch (*Betula pendula*) forest in

Oxfordshire, UK, on one windy and one calm day. Fluctuations in UV-B radiation in Panel D are the result of wind-driven changes in canopy leaf flutter. Figure from Barnes*, et al.* [322] with permission.

The disruption of plant canopy structure (e.g., due to fire or drought-induced tree mortality) alters the amount and spectral composition of sunlight penetrating canopies (i.e., ratios of UV-B:UV-A:PAR), but the specific changes depend on the type of canopy and vertical position (e.g., crown *vs* understorey).[323] Recent studies using array spectrometers have captured rapid changes in the sun-shade environment under canopies by recording multiple spectra every second.[324] These measurements at high temporal resolution have confirmed findings from earlier studies[282, 325, 326] that the spectral composition as well as total irradiance differs between sun flecks and understorey shade in forests and crop canopies. The importance of this fine-scale temporal and spatial variation in UV radiation in understorey environments for plant growth and development is not entirely clear at present (but see Krause*, et al.* [327,] Krause*, et al.* [328]). There is evidence, however, that plants use the total irradiance received or modulated as cues,[329] which can prime them for seasonal or periodic changes. This may therefore be an important aspect of UV acclimation in understorey species that could lead to better adjustment to conditions of variable UV radiation resulting from modified overstorey canopies brought about by climate change.

Light tends to penetrate canopies more effectively under overcast or hazy sky conditions when the ratio of diffuse to direct radiation is higher, than under clear sky conditions.[330-332] Thus, cloudy conditions produce short-term increases in photosynthesis at the whole canopy level.[333-335] However, because leaves that develop in the sun are more efficient in using direct than diffuse radiation, and efficiency of leaves that develop in the shade does not differ significantly under changing sky conditions[336], caution must be exercised in generalising from these results. Conclusions that plant productivity will be enhanced by projected increases in diffuse solar radiation resulting from manipulating aerosol levels in the atmosphere to reduce climate change (i.e., geoengineering)[4] must be viewed with a high degree of uncertainty because they will depend on the geographic location, on the extent of the reduction in incident irradiance and whether the increased canopy light-use efficiency from diffuse radiation is sufficient to offset this and persist in the long term.[69]

Remote sensing of vegetation using satellites is routinely used to measure primary productivity and leaf pigments involved in photosynthesis; this technique has been used extensively for the scaling of ecosystem processes related to the carbon cycle.[337] Most of these ecosystem process models have been developed for use in combining leaf-level and remotely-sensed data, but new possibilities to better understand canopy reflectance of UV radiation are being made possible by the capacity to extend these remotely captured images and spectral data into the UV range of the spectrum.

Radiative transfer models used to model canopy optical properties and determine the fate of solar radiation have not yet been extended into the UV range, e.g., the discrete anisotropic radiative transfer model.(DART[338]) These models can incorporate sub-models for leaf optical properties (e.g., PROSPECT-D,[339] and Fluspect-CX), which previously have been applied for optical estimation of chlorophyll and carotenoids but if extended into the blue light and UV-A regions could include estimation of anthocyanins[340] and flavonoids. This may be facilitated by the new generation of those satellites designed for monitoring vegetation, which include the capacity to detect wavelengths spanning into the UV portion of the spectrum (from the European Space Agency, 270-370 nm for Sentinel-5 Satellite and Sentinel-5-precusor satellite). An alternative approach is to extend atmospheric radiative transfer models, such as libRadtran[4, 341] and the tropospheric and visible solar UV radiation model (http://cprm.acom.ucar.edu/Models/TUV/Interactive_TUV/), to include radiative transfer through plant canopies or even greenhouse structures in the same way that DART and other radiative transfer models (RTMs) are being applied for the visible spectrum, or even coupling these two model types together. At the leaf level, both commercial sensors (e.g., Ocean Optics Jaz[342]) and custom-made devices (e.g., Robberecht and Caldwell [343]) have the capacity to measure leaf reflectance in the UV range in both broadleaved and needle-leaved plants.

In crop canopies, planting distance and crop species, or even the cultivar or variety planted, will dictate the canopy architecture and affect the spectral composition and total irradiance reaching the lower leaves. These decisions also have implications for how UV-B radiation affects plant growth and defence at the canopy level in agricultural crops (see Ballaré [153] and section 3.5.3). With a better understanding of the mechanisms by which plants in canopies respond to UV radiation as a part of the incident spectral irradiance over vertical profiles, we can make better-informed management decisions on species and cultivar selection for specific locations.

3.7.3 Phenology and UV radiation

The implications of warmer winters for the seasonal timing of development or phenology have been extensively studied, with findings consistently showing both the emergence of animals[344, 345] and the onset of plant growth[9,10] to occur earlier in the year there is less sunlight (and by definition less UV-B radiation). Although the molecular mechanisms controlling phenology are not fully understood[346], it is known that organisms often use a variety of environmental cues to safeguard against mis-timing of development.[347-349] Differences among life forms in their rate of response to temperature, which is usually the predominant cue, create the potential for a disruption of ecosystem processes through a mismatch in the timing of phenology among co-existing organisms such as plants and pollinators.[350,351] It is likely that warmer temperatures will bring overwintering trees out of dormancy prematurely. This will produce an earlier spring bud-burst, possibly so early in the year that at high

latitudes new leaves receive insufficient sunlight to develop as they normally would do later in the year.[352, 353] This also implies that those plant defences partially regulated by UV-B radiation would be weaker and the benefit of pollinators UV-vision reduced.

This forward displacement of phenology due to warming may also heighten the role of alternative phenological cues (e.g., daylength and spectral quality).[354, 355] In particular, more research is required to better understand interactions between daylength (photoperiod) and cues related to spectral quality (i.e., changes in UV-B, UV-A, blue and red light), both of which are detected by plant photoreceptors. Alterations in the timing of spring phenology, particularly at high latitudes, may expose understorey plants to new light environments in early spring when freezing temperatures may limit their physiological acclimation capacity.

3.8 Tracking changes in past UV radiation over geological timescales using the biochemical signatures of plants

The long-term ecological effects of UV-B radiation over geological timescales are studied by palaeoecologists interested in retrospectively reconstructing solar UV-B radiation. Identifying a reliable proxy for tracking changes in UV-B radiation based on the biochemistry of pollen and spores, would help interpretation of the effects of UV-B radiation on terrestrial ecosystems. However, even then an additional calibration would be required to separate changes in total solar radiation from those of UV-B radiation, and it would be difficult to distinguish whether these changes resulted mainly from stratospheric ozone depletion or other environmental or astronomical factors. Improvements in analytical techniques have reduced the uncertainty associated with reconstructions of solar radiation based on the biochemistry of pollen from ice cores and lake sediments that track changes in past UV radiation over geological time scales.[356, 357] These reconstructions may provide a better understanding of the evolution of the stratospheric ozone layer and its interaction with climate change.[358, 359] However, the extent to which UV-absorbing compounds in pollen can be considered reliable indicators of the past UV-B radiation and reflect changes at high temporal resolutions, depends upon the causative temporally-stable relationship between the accumulation of these compounds in pollen and exposure to solar UV-B radiation being experimentally verified.[360]

The preserved outer walls of fossilised spores and pollen grains are made from sporopollenin, which is highly resistant to degradation over geological time scales and contains the phenolic compounds, para-coumaric acid and ferulic acid. Experiments using supplemental UV-B radiation have found the concentrations of these compounds to be proportional to the incident solar UV-B radiation received by the pollen.[358, 361] Exploiting this relationship, Jardine*, et al.*[359] reconstructed UV irradiance at Lake Bosumtwi, in modern-day Ghana, showing that over a 140-thousand-year period fluctuations in the

concentration of phenolics from grass pollen contained in sediments corresponded with patterns of solar UV irradiance derived from changes in the Earth's orbit over cycles of 19-21 thousand years. The correlation between reconstructed UV-irradiance and phenolic concentration is also evident from pine pollen [362] and spores of the ubiquitous clubmoss *Lycopodium*[363] over broad latitudinal gradients, although this correlation is more robust across local elevational gradients.[360] This is because seasonal and environmental variability and differences in UV-B radiation related to weather patterns (temperature and cloudiness) and canopy shade can confound the relationship.

The lack of standardisation and inter-comparability of samples and sampling techniques is one impediment to the wider use of the above techniques. Improvements in the two analytical approaches used to detect phenolic compounds, i.e., Fourier-Transform (FT) high-throughput infra-red spectroscopy and thermally-assisted hydrolysis methylation (THM) with pyrolysis–gas chromatography mass spectrometry (THM–GC/MS), should allow researchers to obtain more detailed information from pollen samples.[364-366] In the latter case, precision should also be improved by calibration of changes in phenolic compounds against a known concentration of a compound added to the sample as a standard or against another compound within the pollen that does not respond to changes in solar radiation.[365] When used in conjunction with radiative transfer modelling,[367] these approaches show promise in distinguishing past environmental gradients in UV radiation, such as that at the end of the Permian period (*ca* 250 million years ago),[368, 369] from other climate changes across geographical gradients and long-time scales. This has the potential to improve our knowledge of the causes and consequences of stratospheric ozone depletion.

3.9 Key gaps in knowledge

Current gaps in our knowledge of the linkages between stratospheric ozone, UV radiation and climate change and their implications for terrestrial ecosystems are a direct consequence of the complexity of systems characterised by interactive loops that link climatology, meteorology and biology (Fig. 1). The challenge lies in developing integrated approaches to assess the effects of UV radiation against a complex background of rapidly evolving environmental conditions as well as human intervention behaviours. The way in which ecosystems respond to the often-interactive effects UV radiation and other climate change dynamics can have important consequences for the functionality and/or productivity of agricultural and natural ecosystems, but currently leave many unknowns. This emphasises the importance of studying combinations of those environmental factors that often change with UV radiation and which may modify the response of organisms to UV radiation in terms of acclimation and productive growth. Thus far, most research has concentrated on potential interactive effects of UV radiation with temperature and/or drought. Since climate warming continues to increase, a better understanding is needed of the effects of UV-B radiation

and rising carbon dioxide together with other climate variables on natural and agricultural systems. This will then facilitate assessments of future outcomes for ecosystem functioning, conservation of species, and selection of environmentally suitable agricultural crops. While growth chamber studies can make valuable contributions to understanding some of the fundamental mechanisms of plant response to UV radiation, there is still a strong need for many growth chamber studies to be validated in the field for a realistic perspective of how organisms will actually respond in a more natural environment.

The balance between negative impacts and beneficial effects on organisms will determine the current and future adaptation and sustainability of terrestrial ecosystems. Changing exposure to UV radiation and climate change factors will affect plant resistance to pests and diseases, food quality and nutritional quality, as well as potentially modifying the behaviour of terrestrial animals. These changes may also affect visual cues contributed by UV radiation for certain animals. However, more information is required to evaluate the possible implications in the context of animal response to future environments and in plant-pest and plant-pollinator interactions, which will have a bearing on food security.

While qualitative analysis of responses to UV radiation and other variables is usually possible, quantitative analyses are often lacking due, in part, to the complexity of diverse and constantly changing biological systems. For example, it is difficult to quantify the importance of processes such as photodegradation and microbial breakdown of terrestrial plant litter for soil carbon storage and emissions at regional and global scales, and their potential contribution to global warming and nutrient cycling.

Climate change together with changes in land-use will very likely continue to have strong impacts on the exposure to UV radiation of ecosystems and terrestrial organisms, including human populations. On a global scale, there is currently insufficient information on the relative contribution and implications of stratospheric ozone depletion to climate change in the southern hemisphere, and how much can be attributed to natural variability. These interactive effects need to be evaluated for the way in which they may continue to modify ecosystem response differently in a future with a recovering stratospheric ozone layer. In addition, emerging findings from stratospheric ozone monitoring need to be taken into account for evaluating the possible implications of any sudden change towards the projected path of ozone recovery. This was recently illustrated in a report[370] suggesting that there are unexpected indications that emissions of the banned ozone-depleting compound, chlorofluorocarbon-11 (CFC-11), have increased. The magnitude and future significance of the responses of terrestrial ecosystems to increasing or decreasing UV radiation, either

dependent or independent of stratospheric ozone depletion, and in the context of climate change, remain largely unknown.

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